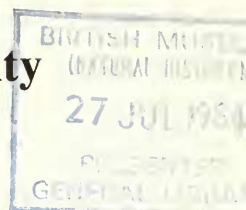


Silicified brachiopods from the Viséan of County Fermanagh, Ireland (III). Rhynchonellids, Spiriferids and Terebratulids

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Synopsis

The description of acid-developed silicified brachiopods from Viséan limestones near Derrygonnelly, County Fermanagh, Ireland, is completed. The taxa belong to the Rhynchonellida, including the Stenoscismatacea, the Spiriferida and the Terebratulida. New taxa are *Propriopugnus* gen. nov., type

species '*Pugnax*' *pugnus* (Martin 1809); *Cyrtina hibernica* sp. nov.; *Minythyra lopa* gen. et sp. nov. and *M. ernea* gen. et sp. nov. in the new family Verneuliidae; *Cryptonella minranensis* sp. nov.; *Girtyella carrickensis* sp. nov.; *Alwynia reidi* sp. nov. and *Beecheria treakensis* sp. nov. Lectotypes are selected for four J. Phillips species, *Terebratula radialis*, *Spirifer ovalis*, *S. integrigosta* and *S. insculpta*; also of *Terebratula ulothrix* de Koninck, *Spirifer carlukensis* Davidson and *Merospirifer insolita* Reed. Neotypes are selected for *Terebratula trilatera* de Koninck, *Spirifer deroissyi* L  veill  , *Tylothyris laminosa* (M'Coy) and *Verneuilia oceani* (d'Orbigny).

The excellence of the silicified material allows detailed descriptions of internal features to be given, and the morphological changes resulting from growth are discussed. Study of the terebratulids points to a much wider diversity of species in British Vis  an rocks than has hitherto been recorded. The composition of the complete fauna of brachiopods is presented.

Introduction

This paper describes the third and last part of the brachiopod faunas collected principally from two Asbian (D_1 or B_1), Vis  an localities in Co. Fermanagh at the Sillees river and at Carrick Lough (Fig. 1), and extracted by acid development. Brief descriptions of the localities and their geological settings have been published (Brunton 1966a, 1968; Tavener-Smith 1973), but a more

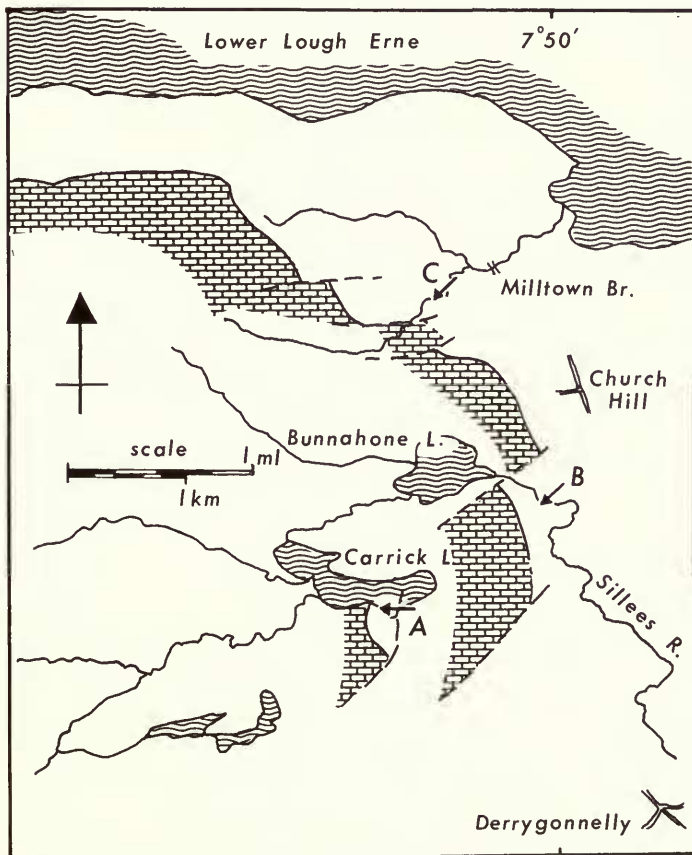


Fig. 1 Map of part of County Fermanagh showing the collecting localities at Carrick Lough (A), near Bunnahone Lough (B) and near Milltown Bridge (C). The arrows also indicate the direction of dip. The small brick symbol indicates areas of lower Dartry Limestone and thus shows its basal junction with the Glencar Limestone. (For the general geological setting see Brunton & Mason 1979).

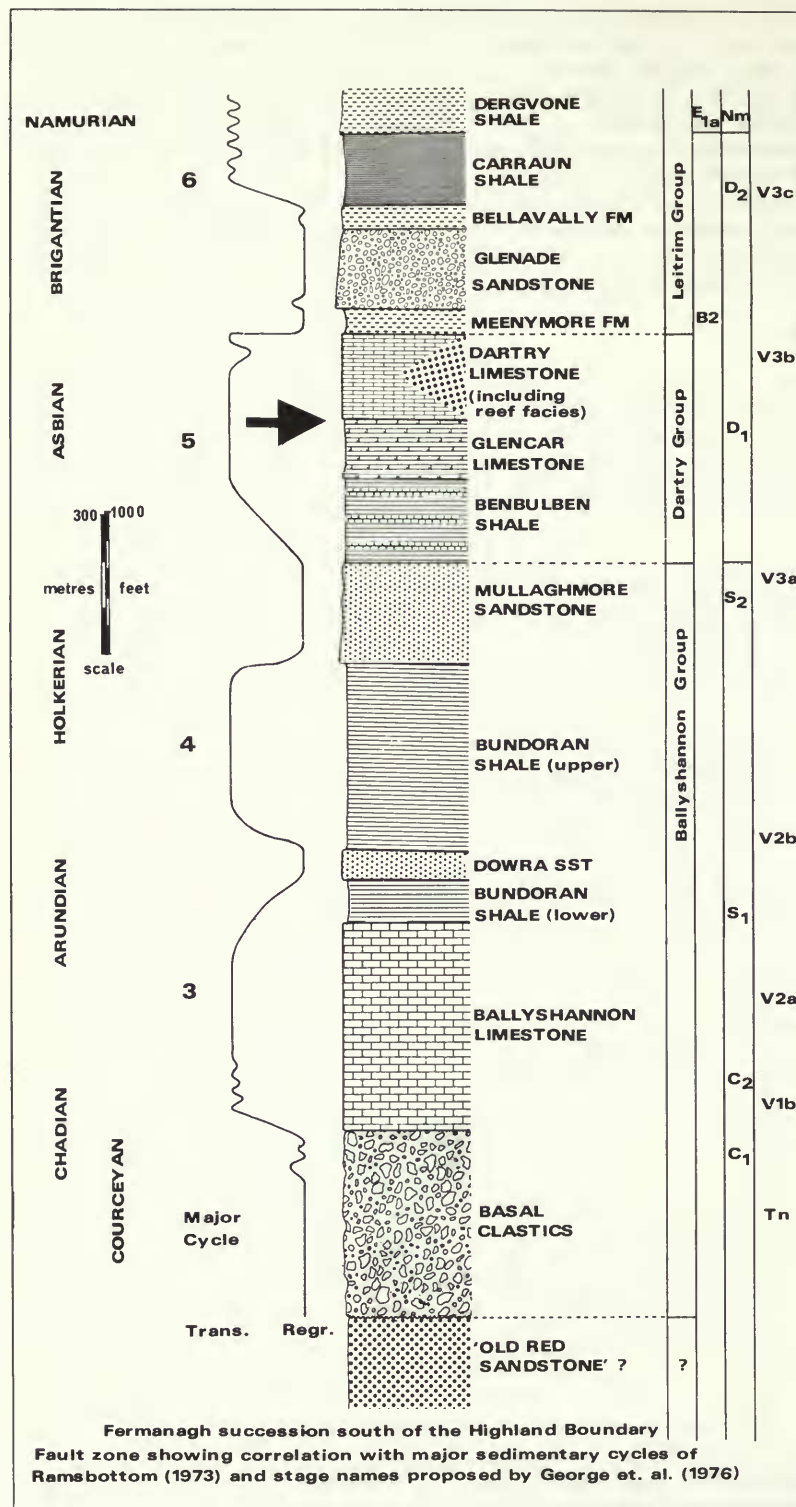


Fig. 2 The stratigraphical succession in County Fermanagh showing the level, in the Asbian, from which the bulk of the faunas were collected. (From Brunton & Mason 1979).

detailed account of the geology of west Fermanagh was presented by Brunton & Mason (1979). The stratigraphical position of the collection localities is shown in Fig. 2; the Asbian (B_1) age has recently been supported by Mitchell & Mitchell (1982).

The two previous Bulletins (Brunton 1966a, 1968) covered the inarticulates, orthids and strophomenoids, a total of 31 species. Here the rhynchonellids, spire-bearers and terebratulids are described, adding 24 species (plus an extra productacean) to the total of 56 recognized brachiopod species. In this study a greater use has been made of comparative material from areas beyond Fermanagh, found to be necessary in determining and describing more accurately some taxa; it also includes the selection of lectotypes for some well-established species. While many of the brachiopods described in Phillips' (1836) important study of the geology of Yorkshire remain without established type specimens, those of his species recognized in the Fermanagh faunas have their lectotypes chosen and figured here, pending a major review of the Yorkshire material still in progress. Two species have already been described, principally from non-silicified material; the endopunctate rhynchonellid *Tretorhynchia trilatera* (de Koninck) (Brunton 1971), and the spiriferid *Fusella rhomboidea* (Phillips) (Brunton & Rissoné 1976).

Because the faunas have been extracted from the limestones by acid digestion the numbers of specimens are large; commonly a species is represented by hundreds of individuals. Also the range in size of specimens commonly covers much of the species' inferred growth, allowing information to be given for the first time on their variability and growth changes. Some species are represented by large numbers of small specimens, which probably indicate the population structure more closely than would specimens collected by traditional methods of cracking out from the rock.

Silicification

The brachiopods from the Fermanagh localities are commonly incompletely silicified, especially if originally thick-shelled, but the silicification is fine in its replacement of the original shell material and usually replicates the major shell fabrics. Thus endopunctuation and pseudopunctuation are commonly recognizable, as seen both at the surface and in broken sections of shell. Similarly, on some specimens, a representation of internal shell mosaic can be seen. These features show that the process was a fine replacement of calcite by silica, not one of total shell solution, followed by silica infilling. The details of external and internal morphologies preserved by silica show that the process started at the surface of the fossils and progressed inwards, following existing fabrics. Some silicified shells are slightly crushed, as if sediment compaction cracked them prior to silicification; silica connects the broken edges. The silicified specimens have, however, also been cracked by regional jointing and it seems likely that silicification occurred during, or closely following, lithification of the rock.

The silicification process was somewhat selective, in that large calcite crystals from crinoids are seldom silicified sufficiently to withstand acid extraction. However, silicification has occurred in the fully calcitic shells of both brachiopods and molluscs as well as in the shells of aragonitic molluscs. Schmitt & Boyd (1981) described patterns of silicification in some Permian brachiopods and bivalves from Wyoming, and Holdaway & Clayton (1982) described late Cretaceous silicified brachiopods from Devon and suggested models for the morphologies of silica they recognized. The Fermanagh brachiopods fall into pattern V of Schmitt & Boyd, which is equivalent to the 'fine textural replacement' of Holdaway & Clayton. Rarely, but slightly more commonly at Boho Quarry, replacement is by beekite rings, or pattern IV of the American authors. Briefly, the Holdaway & Clayton model suggests that the aerobic decay of organic matter raised the partial pressure of carbon dioxide in a restricted microenvironment, and that if silica was in plentiful supply it was precipitated, seeding onto existing shell fabric boundaries, as the calcite was progressively dissolved. Where silica was in limited supply beekite silicification resulted. These authors, and others, have pointed to the differences in dissolution between calcitic and aragonitic shells, the latter tending to be dissolved more completely than the former before the growth of the quartz crystals. This leads to a coarser form of silicification in aragonitic shells, so that many of the Fermanagh molluscan shells are preserved in silica which does not

reproduce the original morphologies as faithfully as in the fully calcitic brachiopod shells. Silicification patterns I to IV of Schmitt & Boyd (1981) result from quartz growths into voids resulting from the dissolution of aragonitic or mixed aragonitic plus calcitic shell fabrics.

Systematic palaeontology

Unless otherwise explained, the classification and terminology used here are as in the *Treatise on Invertebrate Paleontology*, H, Brachiopoda (Williams *et al.* 1965). Descriptive terms for the outline shapes of shells are as suggested by the Systematics Association committee for descriptive biological terminology (Exell & Lewis 1962), and notations in the synonymy lists follow Matthews (1973). Almost all the specimens described and mentioned are in the collections of the British Museum (Natural History), but some are in the University Museum, Oxford (E registration numbers), the collections of the British Geological Survey (IGS registration numbers), the National Museum of Ireland, Dublin (Griffith collection), or l'Institut Royal des Sciences Naturelles de Belgique, Brussels (IG registration numbers).

All the silicified specimens from Fermanagh illustrated here came from the Sillees river locality (14/4B), unless otherwise stated in the figure explanation.

Order **RHYNCHONELLIDA** Kuhn 1949

Superfamily **RHYNCHONELLACEA** Gray 1848

Family **PUGNACIDAE** Rzhonsnitskaya 1956

Genus **PROPRIOPUGNUS** nov.

TYPE SPECIES. *Conchylolithus Anomites pugnus* Martin 1809 (see Muir-Wood 1956).

DIAGNOSIS. Strongly folded pugnacidae with few ribs originating in posterior half, but only fully developed anteriorly. Dental plates short. Small umbonal septalium and wide subhorizontal outer hinge plates with medially separated crural bases.

NAME. Latin *proprius* = genuine, + *pugnus* = fist. Masc.

DISCUSSION. The type species has been assigned in recent years to *Pugnax* Hall & Clark 1893, with *P. acuminatus* (J. Sowerby) as type species. Interiors of *P. acuminatus* were essentially unknown till Schmidt (1965) illustrated serial sections, which were repeated in the *Treatise* (Williams *et al.* 1965: H574) to illustrate *Pugnax*. From those serial sections it is clear that the Fermanagh specimens differ sufficiently to be removed from *Pugnax*. In order to check the differences I have ground the umbones of a specimen *P. pugnus* from the Dinantian limestones of Bolland (BM(NH), B371) which externally resembles the holotype very closely. The internal structures are as in the Irish silicified specimens.

In his study of Mississippian rhynchonellids Weller (1910) illustrated some serial sections called *Pugnax pugnus* (Martin) from the 'Mountain limestone fauna of Ireland'. These sections are good representations of the species, but he did not relate them to the type species, *P. acuminatus*. At that time (1910) Weller erected *Pugnoides* and *Shumardella*; the former tends to be smaller than either *Pugnax* or *Propriopugnus* and is more completely ribbed, while the latter resembles the new genus externally. Internally *Shumardella* differs from the new genus in its strong dental plates and tall persistent dorsal median septum.

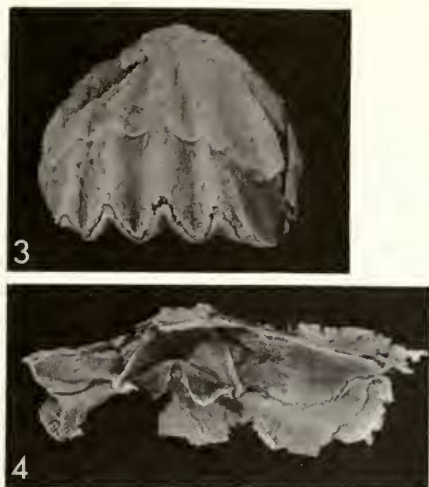
The Tournaisian genus *Ningbingella* Roberts 1971 from north-western Australia resembles *P. pugnus* externally, but internally the Australian genus has a septalium and long, well-defined dorsal median septum which, anteriorly, continues to support the socket ridges and hinge plates.

Propriopugnus pugnus (Martin)

Figs 3–4

v* 1809 *Conchylolithus Anomites (pugnus)* Martin: pl. 22, figs 4, 5.

v* 1951 *Pugnax pugnus* (Martin) Muir-Wood: pl. 4, figs 3a–c.



Figs 3, 4 *Propriopugnus pugnus* (Martin) from the Silles river collections. Fig. 3, an almost complete specimen viewed dorsoposteriorly. BB63645, $\times 2$. Fig. 4, interior of the umbones of an incomplete specimen viewed posteriorly; the ventral valve, with its dental plates, is uppermost. BB63646, $\times 4$.

DIAGNOSIS. In posterior view very broadly obovate. Anterior commissure strongly uniplicate, with three or four ribs within ventral sulcus and up to two smaller ribs on each flank. Short dental plates, close to valve surface; low short dorsal median septum supporting a small septalium in tip of umbo.

LOCALITY AND HORIZON. Martin's original information is 'Carboniferous Limestone – Derbyshire'. A detailed locality cannot be provided, but the age is probably mid to upper Viséan.

HOLOTYPE. Martin's figured specimen is in the Sowerby Collection, BM(NH) B61451, as *Rhynchonella pugnus* Martin. This was recognized as holotype by Muir-Wood (1951) in connection with her submission to the International Commission on Zoological Nomenclature, Opinion 419 (Muir-Wood 1956), upholding Martin's authorship for the species.

DISCUSSION. Sowerby (1825: 156), in discussing Martin's specimen, wrote that its blunt form arose from distortion caused by several fractures. The specimen is certainly fractured but remains essentially undistorted. It is a feature of this species that, once a shell grew to between 15 and 20 mm long, growth directions altered so that the valve margins opposed one another. In this way additional growth thickened the depth of the shell rather than adding much to its length. Parkinson (1954) did not discuss this aspect of growth in his comparative studies of *Pugnax* species. The dimensions of the holotype ($l = 24.5$ mm, $w = 35.4$ mm, $th = 25.5$ mm) differ only very slightly from those of the large specimen (B61218) figured by Sowerby (1825: pl. 497, figs 1).

The species is here transferred from *Pugnax* to *Propriopugnus* on account of its internal characteristics and because the type species of *Pugnax*, *P. acuminatus* (J. Sowerby) (lectotype in the BM(NH), B61235), differs from *pugnus* in possessing a very high, pointed, fold and lacking any well-developed ribs.

The species is represented in the acid-developed faunas from Co. Fermanagh by only a few fragmentary specimens; one incomplete specimen shows the umbonal regions (Fig. 4). Because fragmentation could have resulted from the acid development, these fragments could represent four or five shells as originally preserved in the rock. Two of the more incomplete specimens were filled by crystalline quartz rather than sediment. It seems likely, therefore, that these shells at least were complete at the time of their burial. However, the partially crushed state of some specimens suggests a degree of fragmentation prior to the acid development and it might be that these specimens were carried into the collection site, on the Silles river, prior to burial.

In addition the species is found rarely in the fossiliferous limestones flanking the 'reefs' which developed within the overlying Dartry Limestone.

Genus *PLEUROPUGNOIDES* Ferguson 1966

TYPE SPECIES. *Terebratula pleurodon* Phillips (1836: 222; pl. 12, figs 25, 26), by original designation of Ferguson (1966: 354).

Pleuropugnoides pleurodon (Phillips)

Figs 5–8

DIAGNOSIS (emended). Wide rhynchonelliform shape with strongly serrated uniplicate commissure. Strong ribs originating at umbos, commonly 4 or 5 in ventral sulcus. Dorsal median septum extending anteriorly of sockets, high posteriorly and forming short septalium.

LECTOTYPE. Ferguson (1966) selected as lectotype the specimen figured by Phillips (1836: pl. 12, figs 25, 26), which was collected from Bolland and is in the Gilbertson Collection of the BM(NH), B361. It was refigured by Ferguson when he redescribed the species (1966: pl. 23, figs 1–3).

MATERIAL. The species is poorly represented in the silicified faunas, there being only ten reasonably complete shells from which measurements could be taken. Partially preserved

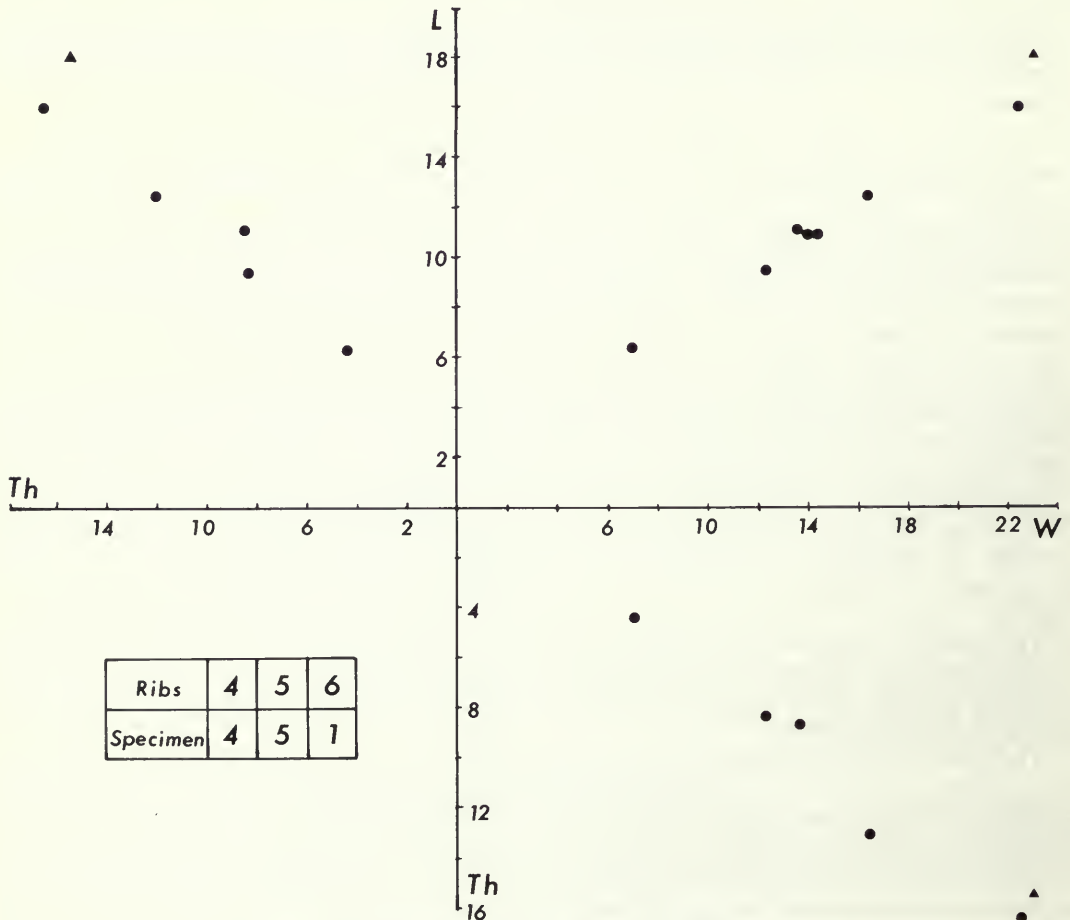
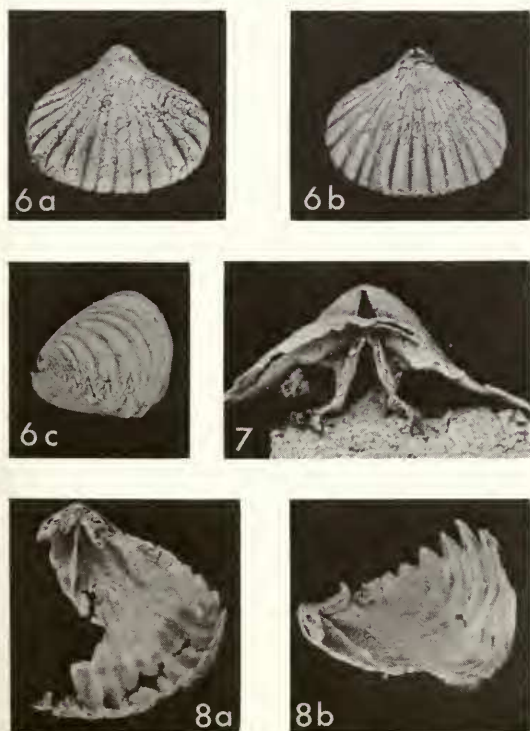


Fig. 5 *Pleuropugnoides pleurodon* (Phillips). Length, width and thickness plots of seven specimens from Co. Fermanagh, plus the lectotype (▲) from Bolland, Yorkshire. Only five of the silicified specimens could be measured for thickness. The table shows the number of ribs counted in the sulcus of ten silicified specimens (cf. Ferguson 1966: 363, table 1).

umbonal regions of two specimens allow some additional information to be given here beyond that of Ferguson's description.

DISCUSSION. The length, width and thickness of the Fermanagh specimens fit closely to those dimensions given for the species by Ferguson. Within the ventral sulcus 4, 5 and 1 specimens have 4, 5 and 6 ribs, whilst the lectotype is atypical in having only 3 ribs in its sulcus. The number of these ribs is a variable characteristic, as can be seen from the Gilbertson Collection specimens (from which the lectotype was chosen), but 4 or 5 ribs is normal (Fig. 5; see also Ferguson 1966: table 1 and Parkinson 1969: table 6). Several of the silicified specimens clearly show that the dorsal median septum extended for up to one-third of the total valve length, well anteriorly of the crural bases (Fig. 8). The septum extends anteriorly to separate the posterior regions of the paired and slightly depressed adductor muscle scars. Posterolaterally of these scars the valve floor is marked by irregular depressions and protuberances, which probably indicate the positions of the genital sacs, as in the living *Hemithyris*. Also, as in living rhynchonellids, the sockets are transversely striated. However, the cardinal process and crura differ considerably from most living representatives. In *P. pleurodon* the dorsal attachment for the diductor muscles is indistinct and seems to have been no more than a roughened area on the apex of the hinge plate; this plate is fused posteriorly with the median septum. The crura extend anteroventrally and their slightly concave blade-like surfaces are orientated at first medially, but anterodorsally towards their tips. The morphology of the cardinalia of these Carboniferous species is more akin to that of the living genera *Compsothyris* or *Hispanirhynchia* than to that of the well-known *Hemithyris* or *Notosaria*.

The somewhat broken condition of the silicified specimens, together with the lack of young individuals and signs of infestations by boring organisms, indicate that they may have remained dead on the sea floor for some time before burial. Closely comparable specimens are locally abundant from 'reef' flanking limestones in the overlying strata. These commonly have six costae in the ventral sulcus but otherwise would seem to be identical to the rare silicified material collected from both the Silles River and Carrick Lough localities. It seems probable that these



Figs 6–8 *Pleuropugnoides pleurodon* (Phillips).

Fig. 6, a young shell in ventral, dorsal and lateral aspects. BB63660, $\times 2$. Fig. 7, the umbonal region of an incomplete shell showing the underside (dorsal surfaces) of the sockets, hinge plates and crura, and the pedicle aperture in the ventral valve. BB63662, $\times 4$. Fig. 8, an incomplete dorsal valve showing the interior viewed dorsally and laterally. BB63661, $\times 3$.

two forms of *Pleuropugnoides* are closely related, but the silicified specimens are sufficiently distinctive to show that they were not derived from some contemporaneous 'reefal' locality.

Superfamily **RHYNCHOPORACEA** Muir-Wood 1955

Most authors assign the rhynchoporaceans to the rhynchonellids on account of their general morphology. It should be noted, however, that Cooper & Grant (1976: 2651) do not assign the superfamily to an order, when describing their abundant silicified Permian species from west Texas, in their belief that the endopunctuation of rhynchoporaceans is of sufficient importance to exclude them from the Rhynchonellida (see Cooper & Grant 1976: 1923). Their view would lead to major brachiopod reclassification. My opinion is that the endopunctate condition in brachiopods is one that appeared and reappeared in several groups as the result of genetical changes, as it were switching on or off the coding for the growth of mantle caecae, which led to the endopunctate shell condition. If this were so then I feel it would be better to retain the otherwise similar rhynchoporaceans within the Rhynchonellida.

Family **RHYNCHOPORIDAE** Muir-Wood 1955

Genus **TRETORHYNCHIA** Brunton 1971

DIAGNOSIS. Outline subtriangular, profile somewhat flattened with thickness just over half width. Anterior commissure rectimarginate. Eighteen to twenty-two strong angular costae on dorsal valves, ventral valves with median costa. Dorsal median septum and wide septalium with vertically disposed blade-like crura. Dental plates short.

This genus was established by Brunton (1971) with type species *Terebratula trilatera* de Koninck from the Viséan of Belgium. The species was described utilising solid specimens from the Viséan 'reefal' limestones of Derbyshire and Staffordshire as well as from other localities in the north-central area of England, north Wales and a possible subspecific variant from the south of Ireland. Internal morphology was based on information from serial sections. The acid-developed Fermanagh faunas contain several broken adults and approximately 35 juvenile specimens, mostly less than 3 mm long. Well-preserved valve interiors are available and although it remains unnecessary to emend the generic diagnosis of 1971 further information can now be presented.

Tretorhynchia trilatera (de Koninck)

Figs 9–20

- 1843 *Terebratula trilatera* de Koninck: 292; pl. 14, figs 7a–d.
 v. 1887 *Rhynchonella trilatera* (de Koninck) de Koninck: 50; pl. 16, figs 68–83.
 1971 *Tretorhynchia trilatera* (de Koninck) Brunton: 99; pls 11, 12.

DIAGNOSIS. Outline approximately equilateral triangular with rounded anterolateral margins. Flattened posterolateral flanks. Costae strong, angular, commonly 18–22 on dorsal valves, median rib on ventral valves. Endopunctate.

NEOTYPE. That figured by de Koninck (1887: pl. 16, figs 69–75) in the Brussels Museum, no. IG 2738b (Brunton 1971: 99) is here selected neotype.

DESCRIPTION. The silicified material largely supports the description given in 1971 but allows the internal morphology to be described more fully from direct evidence rather than from the sets of serial sections used previously.

Within the ventral valve the dental plates converge slightly from below the teeth onto the valve floor (Figs 14, 18), and a faint median ridge, or myophragm, extends anteriorly from between their bases. The teeth are somewhat recurved and crytomatodont (Jaanusson 1971), typical of the Rhynchonellida (Figs 9a, 20).

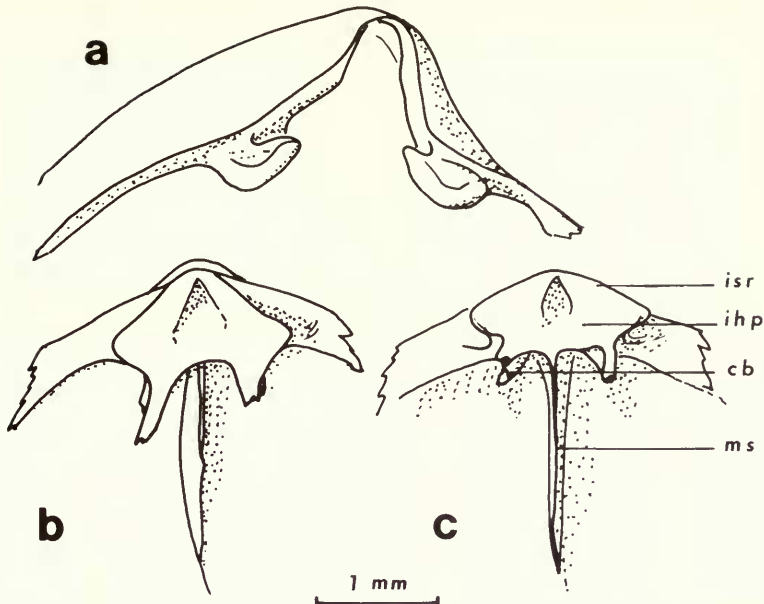


Fig. 9 Drawings from silicified specimens of *Tretorhynchia trilatera*. Fig. 9a, ventral valve umbo showing the crymatodont teeth and open delthyrium (see also Fig. 20). Fig. 9b, c, the cardinalia within a dorsal valve looking dorsally and posterodorsally. isr = inner socket ridge; ihp = inner hinge plate; cb = crural base, and ms = median septum (see also Fig. 12a-c).

The dorsal cardinalia are essentially as previously illustrated (Brunton 1971: 105, text-fig. 16) but the following differences should be noted. The inner socket ridges follow the valve edge closely, overhanging the sockets, and the inner hinge plates recurve posteriorly, at the point of their fusion with the median septum, more than was indicated (Figs 11, 12). The crura are blade-like, in the vertical plane, at their junction with the hinge plates and their development can be traced posteriorly as ridges (crural bases) on the dorsal surface of the hinge plates (Brunton 1971: 101, text-figs 6-8 and Fig. 10 herein).

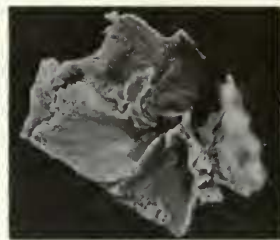
A deep pit between the posterior ends of the inner socket ridges is interpreted as the site of attachment of the diductor muscles. During ontogeny the inner hinge plates grew to about 0.8 mm long, by which time the shell was 5-8 mm long, and thereafter only the articulation structures, crura and median septum grew anteriorly. Thus in juvenile shells the sockets and teeth are situated lateral to the anterior edges of the hinge plates, while in adult shells the teeth are positioned well to the front of the hinge plates and bases of the crura. This anterior migration of the points of articulation enhanced the efficiency of the lever system used by the diductor muscles in opening the shell. In this way the diductor muscles may have retained efficiency as the shell increased in size without having to increase their muscle fibre content to any great extent.

The crura extend to a length of at least 1.5 mm from the dorsal umbo, a little more than suggested in 1971, and they curve ventrally in an arc. Distally, the crura are wide and somewhat concave anterodorsally. The median dorsal septum is about 2 mm long in valves about 9 mm long and remains at this length during any further growth of the valve.

ONTOGENY. Twenty-three juvenile shells ranging in length from 1.5 mm to 4.0 mm were measured. Incomplete valves indicate that specimens of about 10.0 mm long were present in the assemblage. The plotted measurements of 23 specimens extend the plots of length, width and thickness of the non-silicified material (Brunton 1971: 103-4, text-figs 13-15) towards zero. Of 14 dorsal valves on which the ribs could be counted with confidence, 2, 6, 3 and 3 specimens had 15, 16, 17 and 18 ribs. On the non-silicified material previously studied the mean value was 18 dorsal ribs, with a maximum of 24 on 3 specimens out of 43. The ribs over the dorsal and ventral



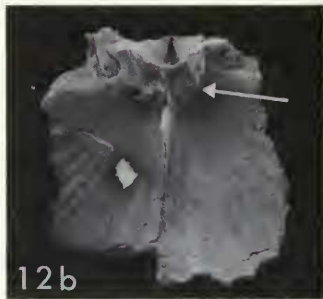
10



11



12a



12b



12c



13



14a



14b



15



16



17a



17b



18a



18b



19a



19b



19c



20

surfaces of *T. trilatera* are normally true costae, the branching or addition on ribs beyond the first mm being extremely rare (Fig. 19). Laterally, on the sides of the umbones, two or three pairs of ribs may have developed while the shells were between 4 mm long and adulthood. On three well-preserved specimens 4 mm long the full 18 costae can be counted. Thus the fewer ribs on the silicified specimens correlates with their smaller size and juvenile condition.

DISCUSSION. As with Recent rhynchonellides, the adult dorsal umbo is tucked into the delthyrial opening of the ventral valve so that in the act of opening the pedicle aperture was not obstructed. The delthyrium (pedicle aperture) remained open and presumably functional throughout ontogeny (Figs 17a, 19a). Very rarely the slight development of deltidial plates confined the aperture to some extent. No signs of abrasion have been recognized at the umbones, such as would be expected had the shells been attached to a hard substrate in a high-energy environment. The restraints of the articulatory processes probably allowed a gape of no more than 25° in living *T. trilatera* and the specimens are thought to have lived on a soft substrate attached to small shelly fragments of bryozoans or brachiopods. Few bored shells have been observed (but see Figs 17b, 20) and the only ones showing any signs of infestation are fragments of old shells which may, therefore, have been invaded after the death of the brachiopod.

The Fermanagh occurrence of *T. trilatera*, from rocks of low D Zone age, does not extend the mid to upper Viséan stratigraphic range given in 1971, but slightly extends to the north-west the known geographical range. In addition, the species has been recorded from Breedon, Leicestershire, by Monteleone (1973).

Superfamily STENOSCISMATACEA Oehlert 1887 (1883)

The taxonomic position of the Stenoscismatacea is not agreed universally. Rudwick (1970) derived the superfamily from the Pentameracea, but the more common view is that adopted by Grant (1965) in placing stenoscismataceans within the Rhynchonellida. Preliminary observations on the shell structure of *Coledium* indicate a standard sequence of a thin primary shell layer followed by a thicker, coarsely fibrous secondary layer. This is as in rhynchonellaceans, whilst the shell structure of some pentameraceans is complicated by the addition of a tertiary layer, more akin to the situation seen in many spiriferids.

Members of the superfamily have only rarely been recorded from Carboniferous rocks in Britain. In older literature species now assigned here might appear under the Camarophoriacea (e.g. Sibly 1906, *Camarophoria isorhyncha* (M'Coy) or *C. globulina* var. *rhomboidea* (Phillips) in Davidson, 1861). Stenoscismatacea species are recorded infrequently in faunal lists under

Figs 10–20 *Tretorhynchia trilatera* (de Koninck). Fig. 10, stereoscopic pair of photographs showing the posterior internal morphology, with the ventral valve uppermost. The crus on the left is almost complete; that on the right is broken and exposes the socket and tooth. BB63666, $\times 5$. Fig. 11, incomplete dorsal valve interior, with a tooth still in place on the right side. BB63668, $\times 6$. Fig. 12a–c, scanning electron micrographs (S.E.M.) of an incomplete dorsal valve interior (plus a tooth in the left socket) showing the median septum and cardinalia, including the thickened crural bases below the hinge plates (arrowed). BD174, $\times 6.7$, 8.5 and 7.5 respectively. Fig. 13, incomplete young shell viewed laterally. BB63669, $\times 3$. Fig. 14a, b, incomplete young ventral valve viewed posteriorly to show the dental plates, and ventrally. BB63670, $\times 3$. Fig. 15, incomplete ventral valve viewed laterally to show the median face of the dental plate, on which growth lines are distinguishable. BB63665, $\times 8$. Fig. 16, S.E.M. dorsal view of a juvenile specimen showing the early dorsal folding and anterior margin. BD177, $\times 11$. Fig. 17a, b, dorsal and ventral valves of a juvenile specimen showing the juvenile outline and accentuated ventral median rib (cf. Fig. 19b). BB63664, $\times 10$. Fig. 18a, b, S.E.M. of incomplete ventral valve showing the cyrtomatodont teeth and dental plates. BD175, $\times 5.6$ and 4.7 respectively. Fig. 19a–c, adult specimen from Wetton, Staffordshire, viewed dorsally, ventrally and laterally. BB58455, $\times 3$. Fig. 20, S.E.M. of young ventral valve interior showing the hook-like teeth; traces of the endopunctuation can be seen on the internal surface anteriorly. BD178, $\times 8.7$.

non-stenoscismatacean genera, and were first fully described in British literature within the modern concepts of the group by Brunton & Champion (1974). Martinez-Chacon (1977) has described stenoscismatacean brachiopods from the Upper Carboniferous of Spain.

Family **STENOSCISMATIDAE** Oehlert 1887 (1883)

Genus **COLEDIUM** Grant 1965

TYPE SPECIES. *C. erugatum* Grant 1965, by original designation; from the Moorefield Formation, Meramec, Mississippian of Oklahoma, U.S.A.

Grant's (1965) important monograph on the superfamily, upon which the *Treatise* (Williams *et al.* 1965) section is based, included the descriptions of *Coledium globulinum* (Phillips), a Permian species, and figured specimens assigned to *Coledium rhomboideum* (Phillips). The specific name *pleurodon* Phillips should not be included within *Coledium*, as it forms the type species of a true rhynchonellacean genus, *Pleuropugnoides*. *C. globulinum* (Phillips) was named only in a plate explanation (Phillips 1834) and the species was not described until Davidson's monograph (1858). Phillips' plate explanation indicates that he intended the species for a Permian fossil, although the name appears neither in his list of Permian (1834: 617) nor Carboniferous (1834: 1605) fossils. I have not been able to recognize any specimens of this species known to have been seen by Phillips. Phillips' specimens of *C. seminum* (Phillips, 1836) are in the British Museum (Natural History), London, and came from Viséan rocks of Bolland (Fig. 21). Both Davidson and Grant considered these species synonymous and from external characteristics this seems possible, despite the resulting long time range. However, there is a difference in the ribbing and

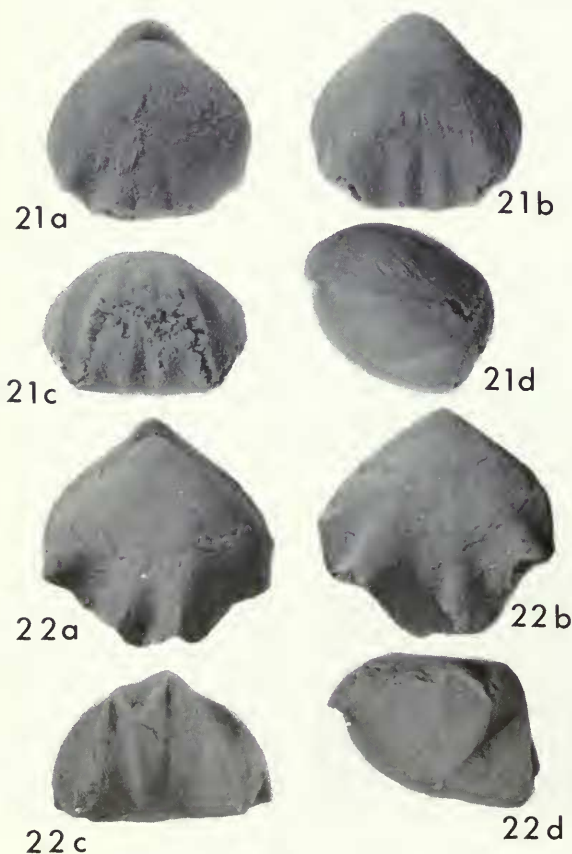


Fig. 21 *Coledium seminum* (Phillips). Lectotype, selected Brunton & Champion (1974), viewed dorsally, ventrally, anteriorly and laterally. Viséan of Bolland, Yorkshire. B355, $\times 6$.

Fig. 22 *Coledium rhomboideum* (Phillips). Lectotype herein selected, viewed dorsally, ventrally, anteriorly and laterally. Viséan of Bolland, Yorkshire. B354, $\times 3$.

folding: out of the 9 specimens of *seminula*, seen by Phillips, 8 have 3 ribs on the dorsal fold whilst out of 17 Permian specimens from Co. Durham assigned to *globulina* 16 have a smooth to 2-ribbed fold and only one specimen closely resembles *seminula* in this feature. All specimens are of the same order of size (5–7 mm long). Comparative studies of interiors are required before relating these species, but it seems likely that there are sufficient morphological differences within this group of *Coledium* to warrant specific separation.

Davidson (1861: 115) synonymized Phillips' three species *globulina* 1834, *seminula* 1836 and *rhomboidea* 1836, believing the first two names to represent the young of *rhomboidea*. At the size attained by most specimens of *seminula* (about 5 mm long), specimens assigned to *rhomboidea* (Fig. 22) do not show ribbing deflections of the anterior commissure, although it is already unisulcate. Furthermore the relative thickness of *seminula* is greater whilst the relative width of *rhomboidea* is slightly greater. *Coledium rhomboideum* (Phillips) is closely comparable externally to *C. explanatum* (McChesney) from the late Mississippian of the U.S.A. They differ internally in that *C. rhomboideum* has a spondylium supported by a high median septum, while that of *C. explanatum* is sessile and raised on a low median septum anteriorly (Weller 1914: 124). Martinez-Chacon (1977) has pointed out that should *C. globulinum* (Phillips) prove not to have an intercamarophorial plate, the species should be assigned to *Cyrolexis*. In Britain *C. rhomboideum* is known from the D Zone 'reef' limestones of Staffordshire, Derbyshire and the type area, Bolland.

Coledium seminulum (Phillips)

Figs 21, 23–29

v* 1836 *Terebratula seminula* Phillips: 222; pl. 12, figs 21–23.

1861 *Camarophoria globulina* (Phillips) Davidson: 115; pl. 24, figs 13–16.

1974 *Coledium seminulum* (Phillips); Brunton & Champion: 824; pl. 109, figs 1–9.

DIAGNOSIS. Small globose *Coledium*, reaching about 8 mm in length, with three ribs on dorsal fold. Spondylium elevated on low median ridge.

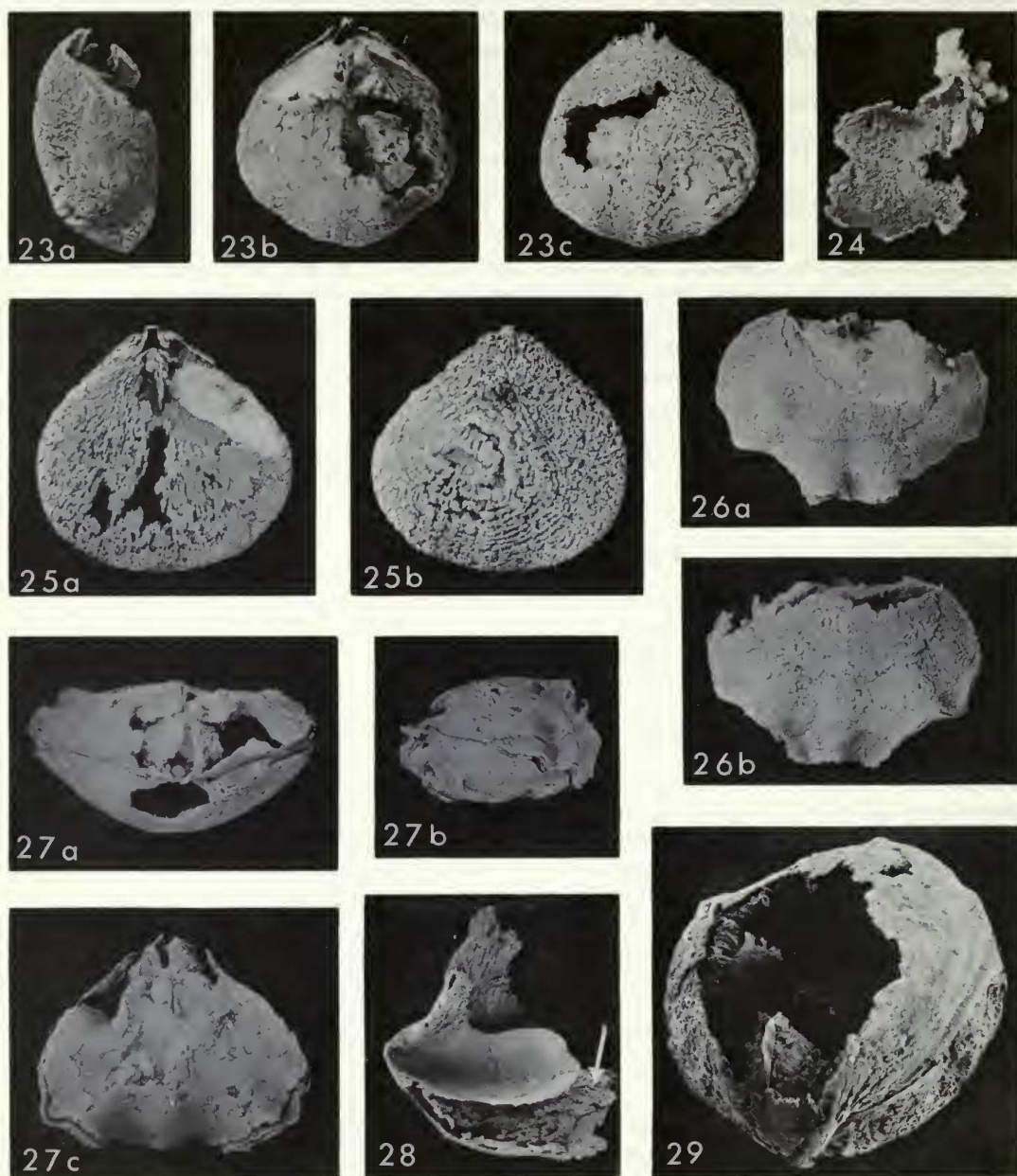
DESCRIPTION. Small globose *Coledium* with subcircular outline. Uniplicate anterior commissure normally modified by three ribs on dorsal fold. Ventral umbo pointed, with narrowly triangular delthyrium directed dorsally. Dental plates fusing to floor of valve, extending anteriorly as slightly expanded spondylium elevated on low median ridge. Short imperforate hinge plate supporting blade-like crura. Camarophorium narrow, curving anteroventrally and supported by high median septum; intercamarophorial plate low and not connecting to hinge plate.

LECTOTYPE. Selected by Brunton & Champion (1974), *T. seminula* Phillips, 1836: pl. 12, fig. 23, from Bolland, Yorkshire. Gilbertson Collection, BM(NH), B355. Figured here as Figs 21a–d.

MATERIAL. Lectotype plus eight other specimens in the Gilbertson Collection from Bolland. Silicified material from the Sillees river locality yields fifteen specimens, many of which are incomplete.

DISCUSSION. Davidson (1861) thought that specimens called *seminula* by Phillips were only the young of Phillips' species *rhomboidea* (Fig. 22). The evidence afforded by the silicified specimens and sections of specimens attributed to *rhomboidea* shows that the internal structures are distinctive and supports the validity of there having been two species. As mentioned above, the spondylium of *C. rhomboideum* is supported on a high median septum from its origin in the beak. The spondylium of *C. seminulum* is sessile, being developed posteriorly from the fusion of dental plates with the valve floor, and only anteriorly it is raised above the valve floor on a low median septum (Figs 28, 29).

The species is insufficiently represented in the Fermanagh faunas to allow conclusive ontogenetic study, but Brunton & Champion (1974) described the growth of the species from specimens collected about one mile west of Wetton village, north Staffordshire. Up to a length of about 3.5 mm the shells grew with a regular, smooth, gently biconvex profile. Beyond this length the plication of the commissure and median ribs developed. Opposed growth at the valve



Figs 23–29 *Coledium seminulum* (Phillips). Fig. 23a–c, lateral, dorsal and ventral views of young shell showing the start of folding at its anterior margin. BB63672, $\times 5$. Fig. 24, incomplete young ventral valve with spondylium. BB63675, $\times 7$. Fig. 25a, b, juvenile shell, before the onset of anterior folding, in dorsal and ventral aspects; in the former, the base of the spondylium and the median septum can be seen. BB63673, $\times 7$. Fig. 26a, b, anterior part of adult shell showing the folding and marginal ribs in dorsal and ventral aspect. From Carrick Lough. BB63620, $\times 4$. Fig. 27a–c, incomplete adult shell in posterior, lateral and ventral views. BB63671, $\times 4$. Fig. 28, internal posterior region of a ventral valve with its spondylium, supported anteriorly on the median septum (arrowed). BD191, S.E.M. $\times 15.5$. Fig. 29, posteroventral regions of young specimen, showing the spondylium. BD1169 (specimen destroyed), S.E.M. $\times 20$.

margins increased the relative thickness of the shell (depth of the body cavity), and the camarophorium grew ventrally. Only in the largest shells, more than about 8 mm long, did lateral ribbing develop.

Being a small species it has probably been overlooked in several localities. Other than the type area, Bolland, and the Fermanagh occurrences I know of the species in north Staffordshire, and in large numbers from the Poyllvaish Limestone near Castletown, Isle of Man, also in Asbian, Viséan rocks.

Order **SPIRIFERIDA** Waagen 1883

Superfamily **RETZIACEA** Waagen 1883

Family **RETZIIDAE** Waagen 1883

Genus **HUSTEDIA** Hall & Clarke 1893

TYPE SPECIES. *Terebratula mormoni* Marcou 1858: 51, from 'Mountain Limestone' strata near Salt Lake City, Utah, U.S.A. Work by Sutherland & Harlow (1973) indicates a Pennsylvanian, Desmoinsian, age for this species.

DESCRIPTION. Broadly elliptical to circular or broadly ovate in outline, subequal biconvex in profile. Equicostate shells commonly lacking fold or sulcus. Deltidial plates conjunct, foramen permesothyridid. Dental plates lacking; with or without pedicle collar. Cardinalia typically with posteriorly recurved median prong-like ligulate process. Jugal lamellae rising anteroventrally and spinose stem projecting posteriorly from saddle.

DISCUSSION. The type species of the genus was well described by Hall & Clarke who figured the cardinalia and part of the spiralia. These authors suggested that the European species *Terebratula radialis* Phillips, *Retzia carbonaria* Davidson and *T. ulothrix* de Koninck should be included in *Hustedia*. The acceptance of *H. ulothrix* within the genus necessitates revision of the generic diagnosis given in the *Treatise* (Williams *et al.* 1965: H652).

Several different species names have been used for shells belonging to *Hustedia* from British and Belgian Lower Carboniferous strata. Davidson, who is well known for his grouping of fossil species, in describing *H. radialis* (1863: 218) wrote that this 'shell appears to have varied considerably in shape, as well as in the number and size of its ribs, so much so that many of its variations when viewed individually might lead us to doubt their being simple modifications of Phillips' type'. He went on to describe how the extreme forms could be linked by intermediate forms. He considered them all to be of the same species and said that he illustrated 'the most marked variations' in his plates. In addition to *H. radialis* Davidson recognized *H. ulothrix* and described for the first time the species *carbonaria**, assigned either to *Retzia* or *Rhynchospirina*. Davidson sent drawings of his species to Hall who later included it in *Hustedia*. By contrast de Koninck (1887) figured six species of *Retzia* which would now be placed in *Hustedia*. All save for *radialis*, which he synonymized with *mormoni*, were his own species; *ulothrix*, *buchiana*, *multiplicata* (*multicostata* is the name used on the plate explanation) and *intermedia*. He did not record *carbonaria*, although Davidson had sent him drawings for comment. *H. ulothrix* and *H. buchiana* are distinct from *H. radialis*, to which the other de Koninck 'species' are closely related, or subspecific variants.

Study of *Hustedia* specimens in the BM(NH) collections shows that the common range in the number of costae on dorsal valves of *H. ulothrix* is 7 or 9, on *H. mormoni* 13 to 15 and on *H. radialis* 18 to 21. (Sutherland & Harlow, 1973, give an average of 14.4 ribs, range 12–17, on 26 specimens of *H. mormoni* from the Desmoinsian of New Mexico.) We have little knowledge of

*The original specimen of *Retzia carbonaria* Davidson (1863: 219; pl. 51, fig 3) is in the IGS collections at Leeds, No. 86028; a replica is in the BM(NH) collection, BB58683. This specimen is partially silicified but can be seen to have been endopunctate from the areas of unaltered shell. Davidson's figures have been restored to some extent but are a close likeness to the specimen, which is 19.6 mm long, 15.8 mm wide and 11.3 mm thick; the dorsal valve has about 21 costae and no costellae are visible. It seems possible that the specimen is an unusually large example of *Hustedia radialis* (Phillips).

the interiors of *Hustedia* species at present described from Lower Carboniferous rocks. The variation demonstrable within a fossil assemblage, such as that from Fermanagh, supports Davidson's (1863) contention that the various forms similar to *H. radialis* should be grouped under that species name. In the future if we have large samples, including the variety of forms at present named, it may be possible to provide distinctive characteristics for several species.

Hustedia radialis (Phillips)

Figs 30–38

- v* 1836 *Terebratula radialis* Phillips: 223; pl. 12, figs 40, 41.
 1861 *Retzia radialis* (Phillips) Davidson: 87; pl. 17, figs 19–21.
 1863 *Retzia radialis* (Phillips); Davidson: 218; pl. 51, figs 4–9.
 1887 *Retzia radialis* (Phillips); de Koninck: 94; pl. 22, figs 16–19.
 (?)1887 *Retzia multiplicata* de Koninck: 95; pl. 22, figs 20–24.
 v. 1974 *Hustedia* cf. *radialis* (Phillips); Brunton & Champion: 825; pl. 109, figs 10–18.

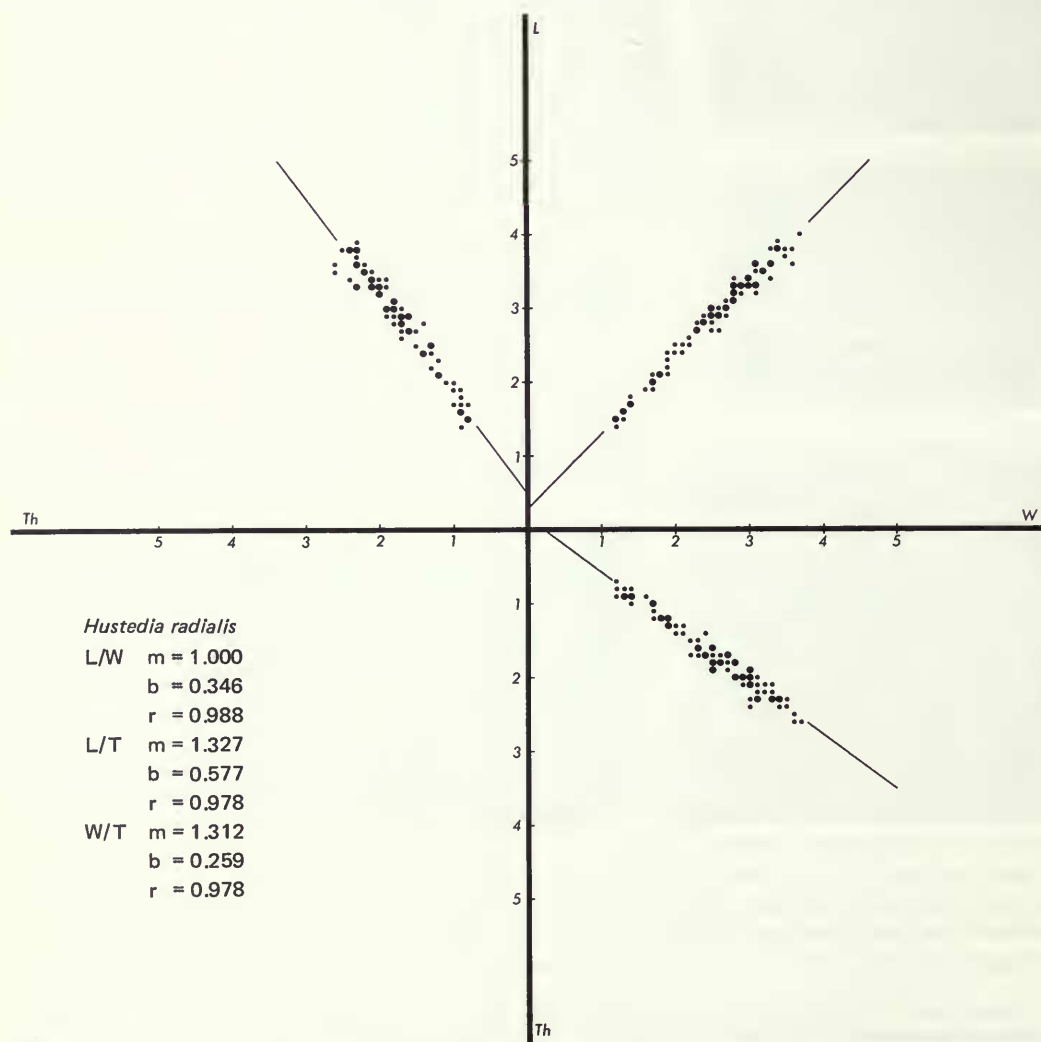
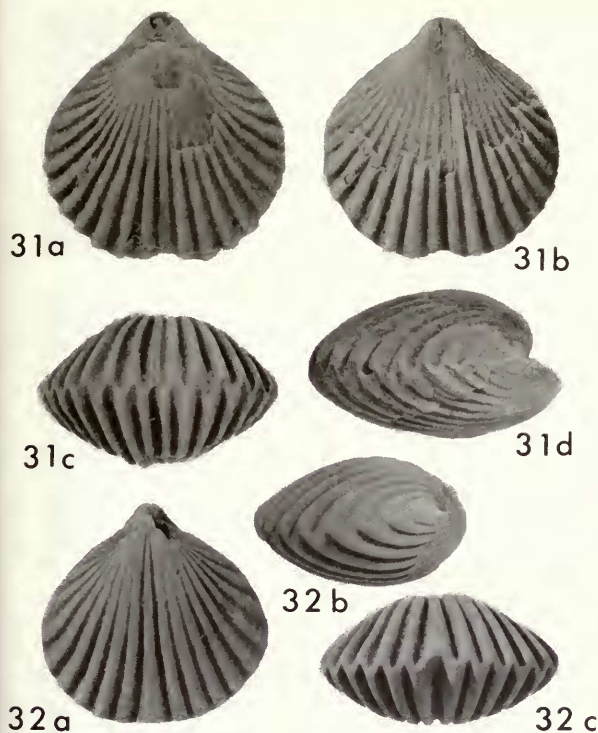


Fig. 30 *Hustedia radialis* (Phillips). Length, width and thickness plots of 90 specimens from Co. Fermanagh. m = slope of the regression line; b = intersection point of m with an axis; r = coefficient of correlation between two attributes.



Figs 31–32 *Hustedia radialis* (Phillips), Gilbertson Collection, Bolland, Yorkshire. Fig. 31a–d, dorsal, ventral, anterior and lateral view of a small paralectotype. BB65230, $\times 6$. Fig. 32a–c, dorsal, lateral and anterior views of lectotype (herein selected). B328, $\times 3$.

DIAGNOSIS. Subcircular to broadly ovate in outline, biconvex in profile. Costate, commonly 19 or 20 costae on each valve (range 17–23), short pedicle collar and cardinalia as for genus, endopunctuation coarse, about 25 per mm^2 on lectotype.

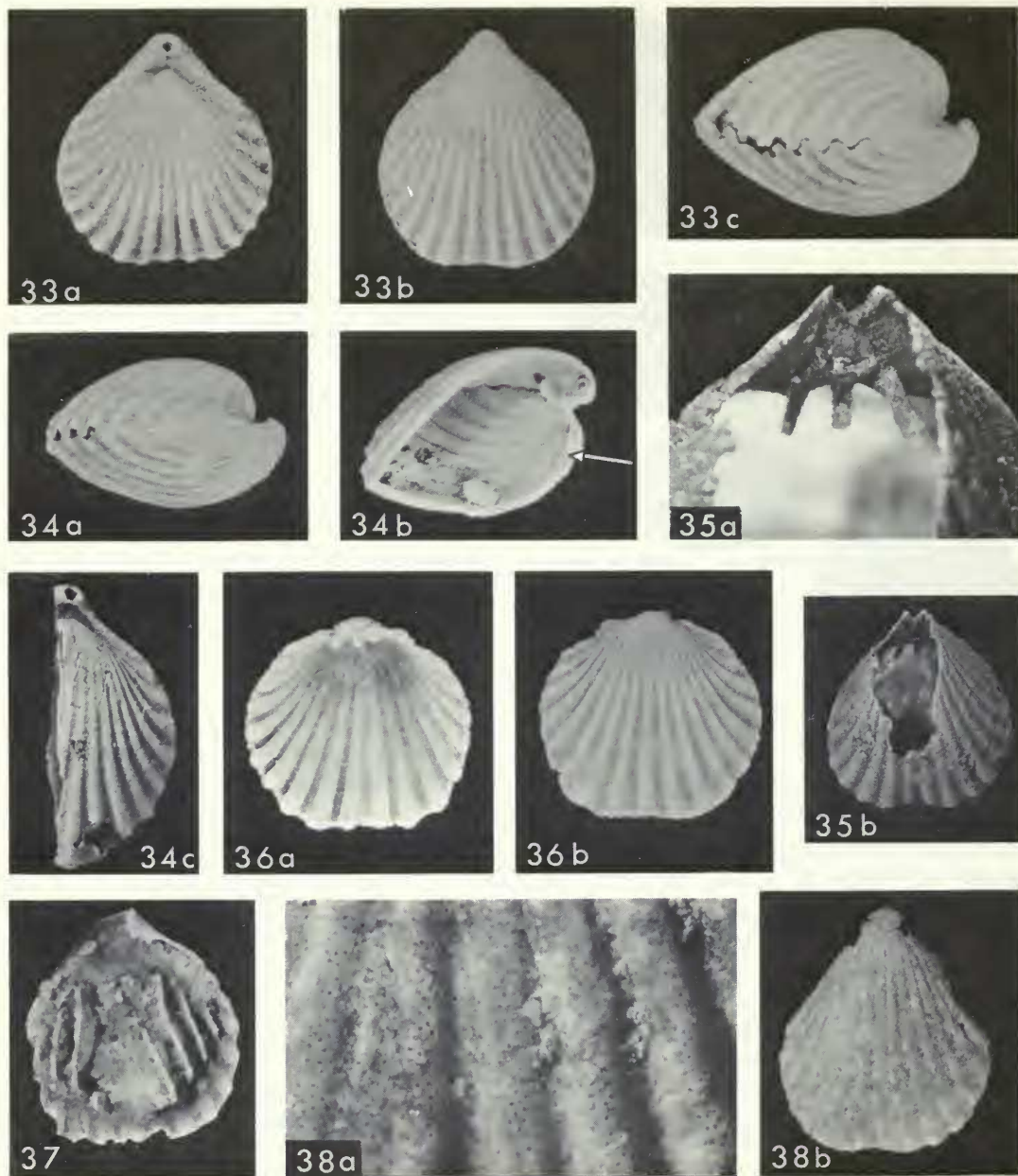
LECTOTYPE. Here selected, from the Gilbertson Collection in the BM(NH), B328; specimen figured by Phillips, pl. 12, figs 40, ?41, from Bolland, Yorkshire (Fig. 32a–c).

MATERIAL. In the Gilbertson Collection there are six specimens from Bolland labelled '*T. radialis* Phillips'. Two are relatively large, the lectotype (Fig. 32) 9.6 mm long, and a second less well-preserved specimen 9.7 mm long. The other four are only about 5.0 mm long (e.g. BB65230, Fig. 31) and are thus much more like the Fermanagh silicified specimens. That the two illustrated specimens belong to the same species is debatable; at present I believe there is insufficient evidence to separate them and accordingly name the Fermanagh specimens *H. radialis*. The lectotype was chosen because it was the specimen figured by Phillips. If in the future the small specimens prove to be distinct they will have to be renamed and *radialis* would then be restricted to the more broadly ovate specimens, which perhaps are characterized by fewer costae, a maximum of 18 dorsal as compared to 23 on the small specimens.

The species is one of the commonest from the etched faunas, there being several hundreds of specimens from the two principal localities at the Sillee river and Carrick Lough.

DESCRIPTION. The Fermanagh silicified specimens are small, ranging from about 1.5 mm to about 4.0 mm long (Fig. 30). The larger, perfectly preserved specimens show 21 dorsal costae. This compares with 18 on the lectotype and 19 or 20 on the second large Gilbertson specimen, and 20 to 24 costae on the four small specimens.

In the ventral valve the deltidial plates are medially fused with no clear line of junction, thus forming a symphytium. The pedicle collar is small and restricted to a thickened rim around the inside of the pedicle aperture (Fig. 34b). Signs of the muscle scars have not been observed in ventral valves. In dorsal valves there is a slight median ridge extending anteriorly from below the hinge plate for about one mm, within the umbonal region. This ridge separated the adductor



Figs 33–38 *Hustedia radialis* (Phillips), from Co. Fermanagh. Fig. 33a–c, adult specimen in dorsal, ventral and lateral views. BB63410, $\times 10$. Fig. 34a, b, half a complete shell viewed laterally, externally and internally, showing the small pedicle collar, part of the cardinal process and the low dorsal median ridge (arrowed). BB63408, $\times 8$. Fig. 34c, same specimen viewed dorsally. BB63408, $\times 10$. Fig. 35a, b, incomplete shell with part of the ventral valve missing, showing the ventral aspect of the three-pronged cardinal process as it curves towards the inner surface of the deltidial plates. BB63412, $\times 25$ and $\times 8$ respectively. Fig. 36a, b, internal and external views of adult dorsal valve, BB63409, $\times 10$. Fig. 37, inside of a ventral valve to which part of the spiralium is stuck by siliceous deposits. BB63413, $\times 10$. Fig. 38a, b, anterior of a ventral valve, without ammonium chloride spray, to show the endopunctuation replicated in the silicified shell. BB63497, $\times 40$ and $\times 10$ respectively.

muscle areas and was present from an early stage of ontogeny. In young dorsal valves about 2.0 mm long the cardinalia would appear to have lacked the median ligulate process. This may be the result of preservation failure in the smallest valves, but by a length of about 2.5 mm there are signs of this process having developed (Fig. 35).

H. radialis appears to be devoid of growth lines, rendering it impossible to check the ontogeny of an individual against the results obtained from the variously-sized specimens in the sample as a whole. One cannot tell if the wider, more circular outline of the large Gilbertson specimens results simply from their larger size. From the available data on external dimensions, growth would seem to have been isometric except in the earliest stages (to about 1.5 mm long) when thickness increased more slowly than later in life.

DISCUSSION. Judged by specimens of *H. mormoni* from the Pennsylvanian of Texas and Kansas in the BM(NH) collections, and from published information by Hall & Clarke (1893) and Sutherland & Harlow (1973), this species differs from the type of *H. radialis* by being more elongate and in having only 13 to 15 dorsal costae. *H. texana* Girty 1926, as described and refigured by Carter (1967), from low Mississippian (high Tournaisian) strata of North America is very similar to *H. radialis*. From Carter's measurements (1967: 322) *H. texana* is about two-thirds as thick as specimens of the same length from Fermanagh, but of very similar relative thickness to the four small specimens in the Gilbertson Collection. Carter writes that he found 'no pedicle collar in sectioned specimens' (1967: 319). Unfortunately his figures do not include the ventral umbo, but if *H. texana* should prove to have a small pedicle collar it seems likely that it would be conspecific with *H. radialis*. Roberts (1971) has described *H. paula* from the Utting Calcarene (= D₁) of north-western Australia, and this species is similar to *H. radialis*. His specimens are small (up to 6.5 mm long) and of the same general shape, but perhaps differ in having only 17 dorsal valve costae (within the range of Fermanagh specimens). The dorsal valve interiors of *H. paula* Roberts are more strongly featured than those of the Fermanagh specimens; the muscle scars, median ridge and vascular ridges all show clearly in his figured specimen (1971: pl. 37, figs 14, 15).

Silicified specimens from Viséan strata in north Staffordshire, assigned to *H. cf. radialis* by Brunton & Champion (1974), are very similar to the Fermanagh specimens in all respects except that they have fewer ribs and the thickness of the shell is slightly less in the Staffordshire material.

Probably because of their small size *Hustedia* specimens are uncommonly recorded in Britain, except from areas in which it has been possible to develop by acid solution of the rock. So far such acid-developed faunas have contained no large specimens like the lectotype. This may be the result of sampling areas which are marginal to the main habitat of this species. Both the Fermanagh and north Staffordshire silicified faunas come from fine-grained, rather argillaceous limestones unlike the 'clean' limestone 'reefal' facies from which the lectotype probably came.

Hustedia ulothrix (de Koninck)

Figs 39–43

- 1843 *Terebratula ulotrix* de Koninck: pl. 19, figs 5 (on p. 292 named as *crispata*; this name recognized as preoccupied and species renamed on plate explanation).
- 1861 *Retzia ulotrix* (de Koninck) (*sic*) Davidson: 88; pl. 18, figs 14, 15.
- 1863 *Retzia ulotrix* (de Koninck) (*sic*); Davidson: appendix pl. 54, fig. 45.
- v* 1887 *Retzia ulothrix* (de Koninck); de Koninck: 92; pl. 22, figs 1–4.
- 1887 ?*Retzia davidsoni* (de Koninck) de Koninck: 92; pl. 22, fig. 10.

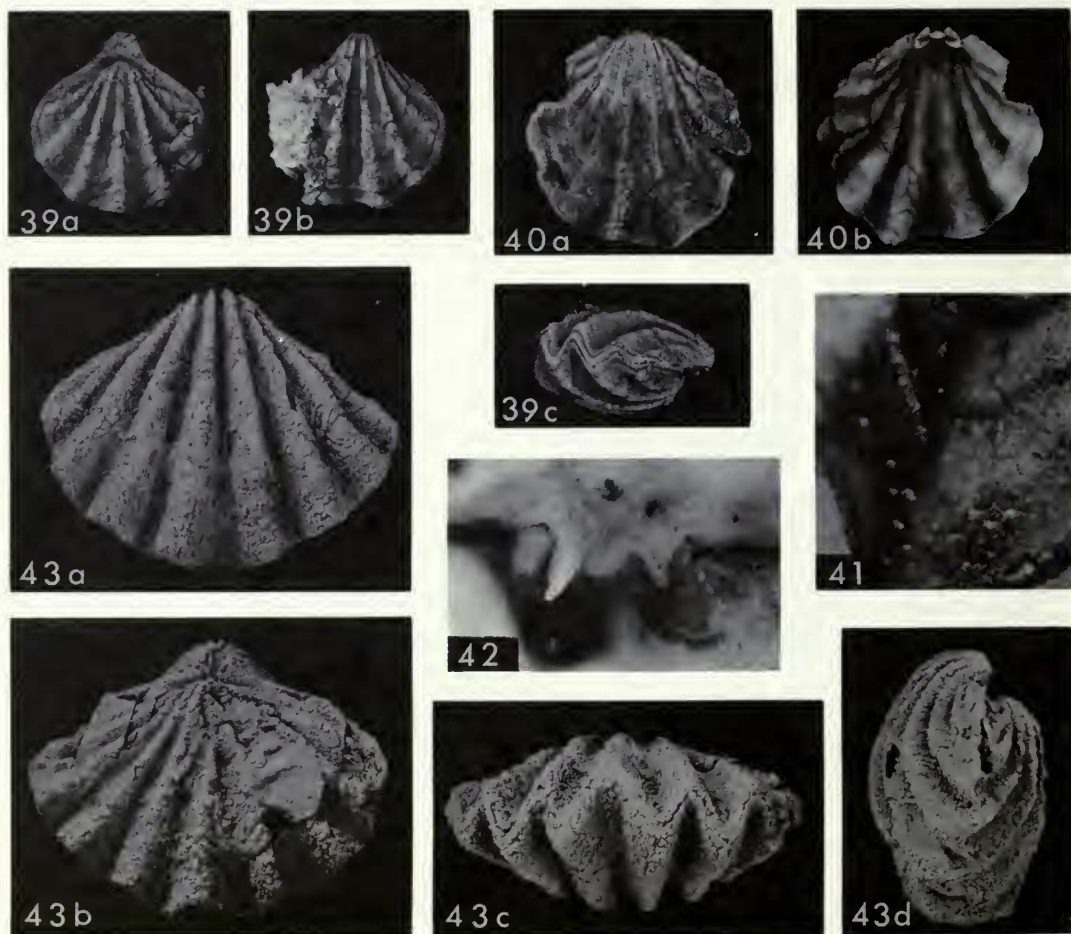
DIAGNOSIS. Coarsely ribbed (7 or 9 on dorsal valves) *Hustedia* with dorsal median rib. Ventral valve with prominent umbo, long interarea and ? lacking pedicle collar. Cardinal process lacking median ligulate process.

LECTOTYPE. The specimen figured by de Koninck (1843: pl. 19, figs 5a–c) as *Terebratula ulotrix*, and again (1887: pl. 22, figs 1–4) as *Retzia ulothrix*, is apparently (de Koninck 1843: 292) one of two originally examined by him. It is here selected lectotype (Fig. 43a–d). It is in the collections

of the Institut Royal des Sciences Naturelles de Belgique, Brussels; cast in the BM(NH), no. BB61404. The four figures of 1887 are different superficially from those of 1843, but on close inspection, along with the chosen specimen, it seems probable that both sets of drawings were made from the same original. I believe, therefore, that the chosen specimen is one of the two originally mentioned by de Koninck.

NAME. The trivial name was first printed as *ulotrix* (de Koninck 1843), as a substitute for *crispata*, in the plate explanation. It seems clear that this was a printers' error, for not only were all subsequent de Koninck references spelt *ulothrix* but labels written by de Koninck use this spelling.

MATERIAL. In the Fermanagh faunas this species is rare. The Silles river locality has yielded only four complete shells plus seven more or less complete valves (4 dorsal, 3 ventral). The largest specimen (7.5 mm long, 7.2 mm wide, 4.0 mm thick) is small by comparison with those in museum collections, a feature common to most species recovered from these limestones. The



Figs 39–43 *Hustedia ulothrix* (de Koninck). Fig. 39a–c, dorsal, ventral and lateral views of young specimen from the Carrick Lough locality. BB63425, $\times 3$. Fig. 40a, b, dorsal valve, exterior and interior, showing the inner socket ridges and relatively simple cardinal process. BB63417, $\times 5$. Fig. 41, part of ventral valve exterior anteromedially, showing the microspinose ornamentation. BB63416, $\times 20$. Fig. 42, anteroventral aspect of cardinalia showing teeth, the strong inner socket ridges and lack of a median process. BB63415, $\times 14$. Fig. 43a–d, **lectotype** (herein selected), from the de Koninck collection in Brussels, viewed ventrally, dorsally, anteriorly and laterally. $\times 3$.

smallest shell is only 3.4 mm long, 2.8 mm wide and 1.6 mm thick. This and other incomplete valves indicate that the sample contains a wide range of sizes of specimen and it seems likely that it represents an assemblage preserved close to the site of the original living population.

DISCUSSION. Two internal morphological features differ from those normal for the genus: the lack of a pedicle collar and the lack of a median ligulate process on the cardinalia (Figs 40b, 42). These features were figured and described in the original description of *Hustedia* by Hall & Clarke (1893) and are repeated in the brachiopod *Treatise* (William *et al.* 1965). The question arises, therefore, whether to widen the generic description to include this species or to suggest a new generic name. The former procedure has been adopted as the gross form of other morphological features is comparable in *H. ulothrix*, *H. radialis* and (from illustrations and specimens in museum collections) *H. mormoni*.

The species is rare and seems only to have been recorded in the British Isles from Bolland, West Yorkshire; Wetton and Alstonefield, Staffordshire (Davidson 1861, 1863); the Settle district of Yorkshire (Garwood & Goodyear 1924); Black Rock, ? Co. Cork, Ireland (Davidson Collection); and from silicified material in the Manifold valley, near Wetton, Staffordshire (Brunton & Champion 1974).

Superfamily **ATHYRIDACEA** Davidson 1881

Family **ATHYRIDIDAE** Davidson 1881

Subfamily **ATHYRIDINAE** Davidson 1881

In the past this family and subfamily have been assigned to M'Coy, 1844 (e.g. Williams *et al.* 1965). However, Alvarez, Brime & Brunton (1980) point out that M'Coy's use of the name 'Athyridae' does not comply with the rules of the International Code of Zoological Nomenclature (Stoll *et al.* 1964), in that it did not, in 1844, contain the generic name *Athyris*. Not until 1881 was *Athyris* placed in the 'Athyridae' by Davidson. Type specimens of several Upper Palaeozoic athyrid species have been selected and described briefly (Brunton 1980), including the type species of two genera in the Fermanagh fauna, *Actinoconchus* and *Cleiothyridina*.

Genus **ACTINOCONCHUS** M'Coy 1844

TYPE SPECIES. *Actinoconchus paradoxus* M'Coy (1844: 150; pl. 21, figs 6a, b). The only species described by M'Coy in his new genus. See Brunton (1980: 221) for details of the species.

DIAGNOSIS. Athyridinae with long, delicate, non-spinose flanges of shell from rugae or strong growth-lines on both valves.

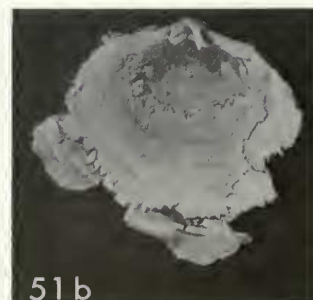
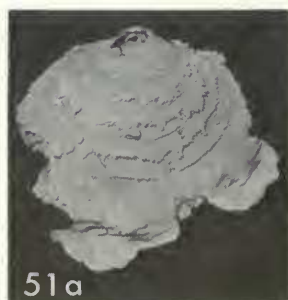
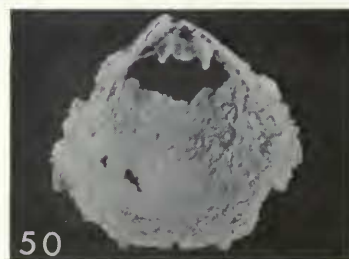
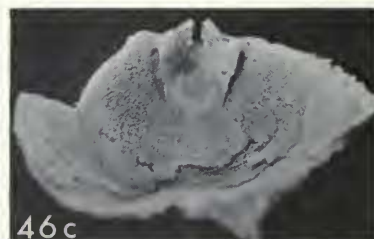
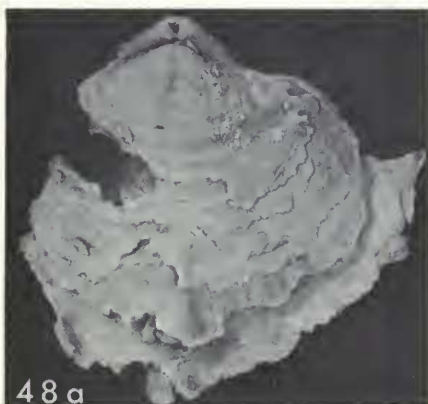
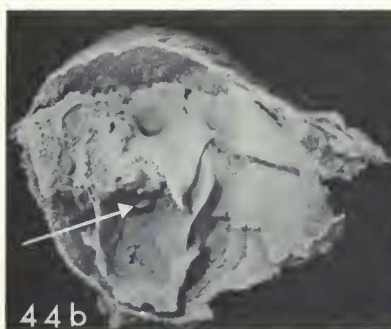
Actinoconchus lamellosus (Léveillé)

Figs 44–51

- 1835 *Spirifer lamellosus* Léveillé: 39; pl. 2, figs 21–23.
- v* 1836 *Spirifera squamosa* Phillips: 220; pl. 10, fig. 21.
- v. 1859 *Athyris lamellosa* (Léveillé) Davidson: 79; pl. 16, figs 1, 1a, b.
- v. 1863 *Athyris lamellosa* (Léveillé); Davidson: pl. 51, fig. 14.
- 1887 *Athyris lamellosa* (Léveillé); de Koninck: pl. 21, figs 1–3, ?4, 5, (?6–8), 11, 12.
- 1965 *Athyris lamellosa* (Léveillé); Boucot, Johnson & Staton in Williams *et al.*: fig. 537, 4b, c, d.

DIAGNOSIS. *Actinoconchus* with depressed obovate outline, ventral sulcus and low dorsal fold with or without shallow sulcus. Shell flanges long and radially corrugated, extending from rugae of both valves.

TYPE SPECIMENS. Léveillé's types appear to be lost (Gaetani 1968: 711). M'Coy (1844: 148) synonymized *S. squamosa* Phillips 1836 (Lectotype B309 in the Gilbertson Collection of the BM(NH), London) with *S. lamellosus* Léveillé 1835. This has been accepted by most subsequent authors. Specimens from Belgium named by de Koninck as *Athyris lamellosa* (Léveillé), now in



the collections of the BM(NH), London, are clearly conspecific with the lectotype of *S. squamosa* Phillips. A neotype for *A. lamellosus* (BM(NH) B20138) was selected by Brunton (1980: figs 16a–d).

DESCRIPTION AND DISCUSSION. This species is uncommon in the silicified Fermanagh faunas, there being five more or less complete shells plus fifteen reasonably complete valves or conjoined umbones. Sizes range from a shell 4 mm wide to one approximately 23 mm wide, excluding the lamellose flanges. Incomplete silicification and the jointing of the rocks has led to some fragmentation during acid digestion. However, the preservation of long and delicate flanges (Fig. 49) indicates that the specimens were not moved any great distance before burial and there is little sign of crushing having taken place. The specimens are considered to be a sample of the brachiopod assemblage that lived in this area.

Descriptions of internal morphology are almost totally lacking for *Actinoconchus* species. Davidson (1882: 98; pl. 5, figs 14–19) described the spiralia of '*Athyris plano-sulcata* of Phillips', in specimens from Castleton, Derbyshire prepared by Rev. N. Glass; one of his figures is reproduced in the *Treatise* (Williams *et al.* 1965: H661, fig. 537.5a). Inspection of these Davidson specimens supports the figures he published. Regretably only one partially-preserved silicified spiralia pair is available, but this shows the hood-like jugum from which the short secondary spires project posterodorsally. It is impossible to be sure of the identification of the specimens prepared by Glass and assigned by Davidson to *A. planosulcata*, but this species and *A. lamellosus*, and possibly *A. paradoxus*, are known from the Castleton area of Derbyshire and as the spiralia of the Athyridinae all seem very similar the specific determination is probably of little consequence.

The silicified specimens of *A. lamellosus* retain well-preserved cardinalia. The cardinal process (Figs 44b, 45) projects posteroventrally into the ventral umbo and is confined laterally by deep sockets, the ridges of which merge posteriorly into the cardinal process and medially overhang the cavity leading to the small cardinal foramen. The structure lacks clear differentiation into hinge plates, socket ridges, etc. owing to its confined median position between the teeth. These are large and supported by well-developed dental plates (Fig. 44b) which became partially buried by secondary shell thickening during the later stages of ontogeny. The posterior dorsal adductor muscle scars are divided medially by a low myophragm. They are elliptical to rhombic in outline and bordered anteriorly by less well-defined elongate anterior scars (Fig. 45b). A pitted area, possibly marking the gonocoel, surrounds the muscle scars laterally and posterolaterally. The ventral adductor muscle scars are narrowly obovate and poorly differentiated medially. The diductor scars are less well-defined but extend widely anterolaterally, as illustrated by Weller (1914: pl. 78, fig. 3, reproduced in Williams *et al.* 1965: H661). Pitting, like that of the dorsal valve, occurs posterolaterally and the ventral valve umbo became progressively thickened on the outer sides of the dental plates until, in old shells, they became almost buried. Between the plates the umbonal cavity remains open and, in life,

Figs 44–51 *Actinoconchus lamellosus* (Léveillé). Fig. 44a, b, umbonal regions of an adult specimen seen externally and internally; the close fit of the dorsal umbo below the ventral umbo can be seen and, internally, the articulation and cardinalia are well displayed, including the apical plate (arrowed) in the ventral umbo. BB43400, $\times 4$. Fig. 45a, b, external and internal views of an almost complete dorsal valve showing the cardinal process, with its small foramen (arrowed), the adductor muscle scars and median myophragm (arrowed), and internal posterolateral ornamentation. BB63399, $\times 3$. Fig. 46a–c, young ventral valve viewed externally, internally and posteroventrally to show the strong teeth and dental plates. BB63402, $\times 5$, $\times 5$ and $\times 6$ respectively. Fig. 47, dorsal view of specimen from the Tournai region of Belgium. BM(NH) 64892, $\times 1$. Fig. 48a, b, dorsal and ventral views of incomplete adult shell with well-preserved pedicle aperture and marginal shelly flanges. BB63398, $\times 2$. Fig. 49, external view of incomplete juvenile ventral valve retaining a large portion of shelly flange medially. BB63403, $\times 5$. Fig. 50, interior of juvenile dorsal valve showing the inner socket ridges, cardinal process (with its foramen), and a piece of ventral valve attached by its tooth on the left. BB63404, $\times 10$. Fig. 51a, b, exterior and interior views of young dorsal valve showing lamellose ornamentation, and the cardinalia. BB63401, $\times 3$.

accommodated the pedicle capsule. Apically, adjacent to where the cardinal process fits between the dental plates, the pedicle cavity of adult specimens has a small anteriorly-projecting plate (Fig. 44b) which would seem to have provided a separation between the pedicle capsule and the diductor muscles, where they were attached to the cardinal process. As the shell opened this little plate fitted closely into the posteromedian groove of the cardinal process.

Athyris bradyensis Carter (1967: 336), from Late Kinderhook limestones (high Tournaisian) of Texas, is similar to *A. lamellosus* externally and seems to have identical lamellose flanges. However, Carter's serial sections indicate a cardinal process different from that of the Fermanagh specimens, and he records a dorsal sulcus, especially in young specimens. A slight dorsal sulcation is normally only seen anteriorly on adult shells of *A. lamellosus*. Within the concepts of *Athyris* and *Actinoconchus* presented here, in which an attempt is made to revert to M'Coy's original definitions, *A. bradyensis* Carter would certainly be placed within *Actinoconchus*, and is closely allied to *A. lamellosus*.

The *Athyris lamellosus* described in the literature from Osagian formations in the central states of the U.S.A. does seem to be conspecific with the European species and may have developed from the older *A. bradyensis* stock of the southern states. If so *Actinoconchus lamellosus* (Léveillé) is known from North America in rocks of mid to upper Tournaisian age; from Britain and western Europe almost throughout the Tournaisian and Viséan, and is recorded from rocks, probably of high Viséan age, in the Moscow basin. Gaetani (1968) records the species from the Tournaisian of the central Elburz. The species has been recorded from China and Jin & Fang (1983) have used material from Yunnan province for the designation of a new genus, *Lamellosathyris*. These authors point out that their *L. lamellosa* lacks the radiating striations so characteristic on the flanges of *A. paradoxus* and that *Actinoconchus*, in their restricted sense, is not strongly folded. Until the Chinese specimens of *L. lamellosa* can be compared with well-authenticated *A. lamellosus* (Léveillé) it is impossible to evaluate *Lamellosathyris*. However, I have sympathy for their differentiation of *A. lamellosus* from *Actinoconchus* and drew attention to some of the differences in 1980 (pp. 225–6).

Genus *CLEIOTHYRIDINA* Buckman 1906

[= *Cleiothyris* King 1850: 137]

TYPE SPECIES. *Atrypa pectinifera* J. de C. Sowerby 1840, by original designation of King, 1850, for *Cleiothyris*, from the Permian of Co. Durham, validated by the I.C.Z.N. (1976). See Brunton (1980: 227) for details.

DIAGNOSIS (emended). Subequally biconvex athyridines with slight dorsal fold and ventral sulcus developed anteriorly. External ornamentation of lamellose growth lines bearing flattened spine-like frills.

DISCUSSION. Buckman (1906) established the genus *Cleiothyridina* as a new name for *Cleiothyris* King 1850. This being so the type species is that designated by King for *Cleiothyris*, *C. pectinifera* (J. de C. Sowerby) (Article 67i of the International Code of Zoological Nomenclature, 1964). This is a Permian species which was thought by some authors to be synonymous with the Carboniferous shell called *Athyris deroissyi* (Léveillé 1835). King remarked that the two bore a striking resemblance. It is probably because he thought the two synonymous that Buckman (1906: 234) designated '*Athyris Royssii*, Davidson, Mon. Carb. Brach. pl. xviii, fig. 8' as type species. Following Buckman the concept of *Cleiothyridina* has been based upon the species illustrated by Davidson (1861: pl. 18, fig. 8), quoted by Buckman, and called '*Athyris Royssii*'. Being somewhat conservative in his systematics Davidson placed several species, including *Spirifera fimbriata* Phillips 1836, into synonymy with '*Athyris Royssii* L'Eveillé', but noted in the plate explanation of pl. 18, fig. 11 that he there illustrated the original Phillips specimen of *S. fimbriata*. This specimen is preserved in the Oxford University Museum (E1093) and it is clear that Davidson's illustrations (1861) on pl. 18, figs 8–11 are of *fimbriata* Phillips, and not *deroissyi* Léveillé, a quite distinct species described and figured by Léveillé (1835: 39; pl. 2, figs 18–20). *Cleiothyridina fimbriata* (Phillips), previously commonly called *C. deroissyi* (Léveillé) (e.g.

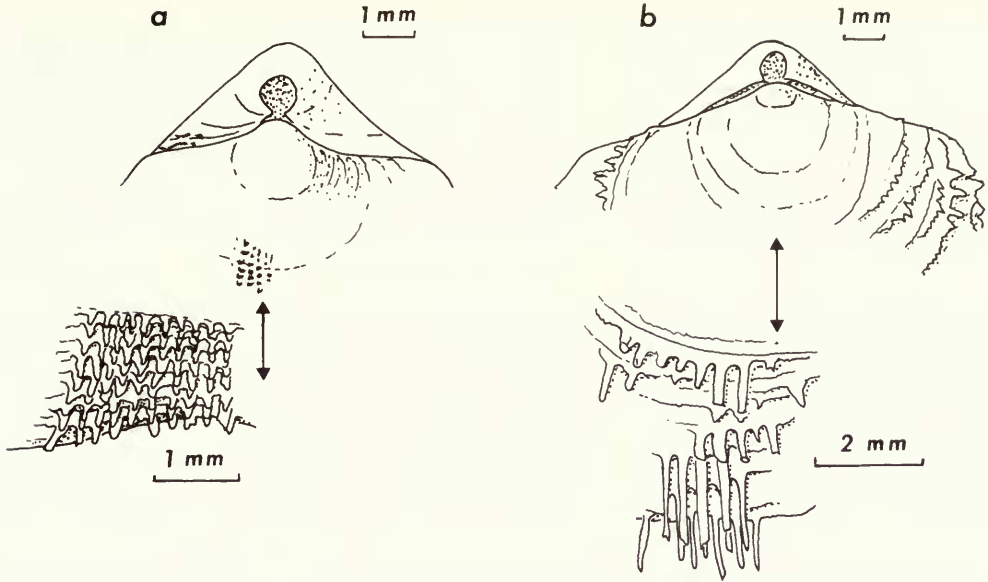


Fig. 52 Drawing comparing the umbonal morphologies and external ornamentations of (a) *Cleiothyridina deroissyi* and (b) *C. fimbriata*. Note the less prominent ventral umbo but stronger and more spine-like ornamentation on the latter (see Figs 62, 67).

Treatise, Williams *et al.* 1965), is closely comparable to the Permian species *C. pectinifera* (J. de C. Sowerby), the type species. Thus although the type species is here corrected to *pectinifera* (for long recognized by Russian palaeontologists), the concept of the genus remains unaltered. Had it been necessary to revert to *deroissyi* Léveillé as type species, the concept of *Cleiothyridina* would have altered, for the difference between *deroissyi* and *fimbriata* is much greater than between *fimbriata* and *pectinifera*. In the silicified Fermanagh faunas both *C. fimbriata* (Phillips) and *C. deroissyi* (Léveillé) are found (Fig. 52).

The I.C.Z.N. (1976) has validated the generic name *Cleiothyridina*, type species *C. pectinifera* (J. de C. Sowerby), and accepted the specific names *fimbriata* Phillips and *deroissyi* Léveillé (Brunton 1972: 142).

Cleiothyridina differs from other Lower Carboniferous Athyridinae in its external ornamentation of concentric, long, spine-like shelly frills. In examples of *C. fimbriata* and *C. pectinifera* these frills are differentiated, especially anteromedially on adult shells, into distinct 'spines' which appear to have had hollow centres. The cardinalia also differ from other Athyridinae in having the cardinal process well differentiated from the hinge plates; in *Actinoconchus* the two are ill-defined and the cardinal process of *Composita* is distinctive. Representatives of *Cleiothyridina* are widely distributed through Lower Carboniferous to mid Permian strata.

Cleiothyridina fimbriata (Phillips)

Figs 53–66

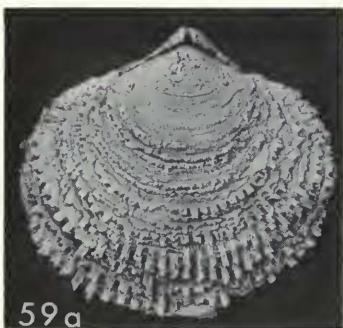
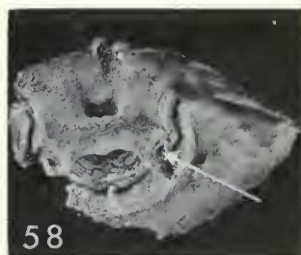
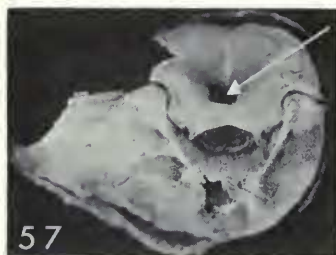
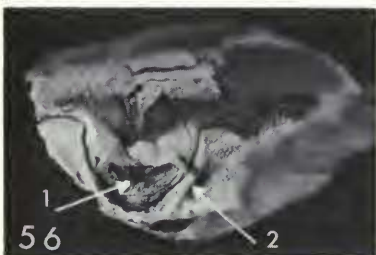
v* 1836 *Spirifera fimbriata* Phillips: 220 (no figs).

1843 *Terebratulula plano-sulcata* (Phillips); de Koninck: 301 (*pars*); pl. 21, figs 1e, f.

v. 1861 *Athyris Royssii* (Léveillé); Davidson: 84 (*pars*); pl. 18, figs 8–11 (fig. 11 from Phillips' original specimen).

v. 1863 *Athyris Royssii* (Léveillé); Davidson: pl. 54, fig. 8.

DIAGNOSIS. Subcircular to transversely broadly obovate in outline, anterior commissure rectimarginate. External ornamentation of concentric thin shell lamellae separating into long recumbent spinose frills.



LECTOTYPE. *Spirifera fimbriata* Phillips, Phillips collection, Oxford University Museum, E1093. From the Lower Carboniferous near Florence Court, Co. Fermanagh, Ireland, probably of early Asbian age (sel. Brunton, 1980: 228).

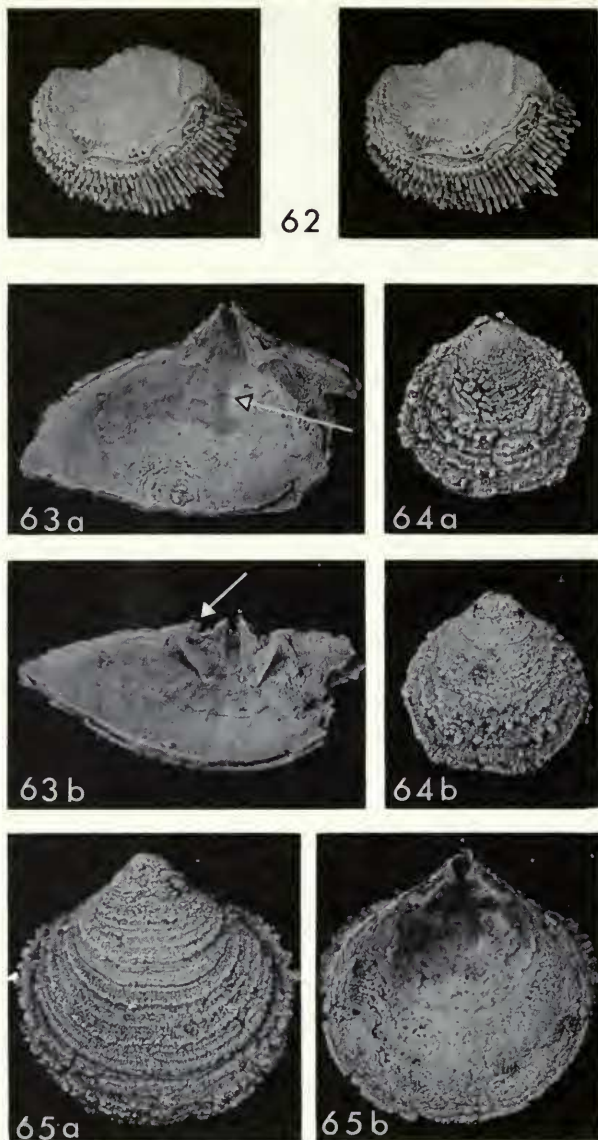
DESCRIPTION. When stripped of its spinose ornamentation the shell is more or less circular in outline, but preservation of these frills commonly adds to the width of the outline posteriorly (Fig. 53a). The umbones are incurved, that of the ventral valve being pointed whilst the dorsal umbo, in all but young shells, is enclosed within the wide, open delthyrium (Fig. 60). In this way the dorsal umbo projected into the ventral valve which the shell was open. In large specimens a short and narrow, flattened, pseudo-interarea may be developed on ventral valves. The commissure is rectimarginate but rarely there is a slight uniplication. Growth lines are marked over the entire shell. Posteromedially the spinose ornamentation is commonly lacking, but peripherally preservation may be good. Each growth line is extended as a thin shelly sheet for a fraction of a millimetre before differentiating into flattened spine-like outgrowths reaching at least 5 mm in length (probably these were much longer while the brachiopod was alive) (Fig. 59). Peripherally, and especially anteromedially (Fig. 62), the 'spines' are well developed and seem to have grown with hollow centres, but no hollow connections to the inner surfaces of the valves were retained. The 'spines' are connected laterally by extremely thin sheets of shell fibres. Posteriorly, lateral to the umbones, the spinose ornamentation is lacking on those regions of the valves which would have impinged against one another when the shell opened (Fig. 61c).

The valve interiors are typically athyridacean. Ventral valves have short dental plates (Fig. 63b), which tend to become buried by secondary shell during late stages of ontogeny, supporting dorsally-projecting, stubby teeth (Fig. 57). Adductor and diductor muscle scars are poorly impressed, the former being narrowly ovate and the latter spreading anterolaterally.

The dorsal cardinalia are approximately one quarter of the total width of the shell. The inner socket ridges curve medially from the valve surface, then ventrally, and their outer surfaces continue ventromedially to form the outer surface of the transversely hemielliptical cardinal process (Figs 53, 55). When the shell is closed the cardinal process fits snugly between the dental plates, within the ventral umbo, and the ridged myophore faces anteroventrally (Figs 56, 58). The short inner hinge plate is entire and recedes posteriorly, but is well differentiated from the sockets and cardinal process. Posteriorly, at the base of the cardinal process, is a small median foramen leading to the cavity dorsal to the hinge plate (Fig. 58). Narrow crura extend anteroventrally from the inner sides of the socket ridges; i.e. there are no well-differentiated outer hinge plates. The dorsal diductor muscle scars form elliptical, slightly sunken areas separated by a low ridge which merges anteriorly into a shallow groove, separating thickened areas of shell. These possibly represent the sites of mantle canals.

The external dimensions of the 28 sufficiently well preserved Fermanagh specimens are given on Fig. 66, on which are also plotted the dimensions of the lectotype.

Figs 53–61 *Cleiothyridina fimbriata* (Phillips). Fig. 53a–c, exterior and interior views of incomplete adult dorsal valve, showing external ornamentation and the cardinalia. BB62976, $\times 3$. Fig. 54a, b, exterior and interior of juvenile ventral valve showing the pedicle aperture and large teeth. BB63454, $\times 6$. Fig. 55, internal view of adult cardinalia, with foramen (arrowed) and adductor muscle fields separated by a low myophragm. BB63451, $\times 4.5$. Fig. 56, internal posterior view of conjoined umbones, showing the close fit of the cardinalia between the adult dental plates; the cardinal process myophore, and foramen, is arrowed (1), as is the crus on the right side (2). BB63447, $\times 4$. Fig. 57, another set of conjoined adult umbones showing the dorsal cavity (arrowed) connecting to the foramen on the myophore surface of the cardinal process. BB63449, $\times 4$. Fig. 58, a pair of umbones from an old specimen in which the dental plates are almost buried by secondary shell; the broken crura are visible (arrowed on the right). BB63450, $\times 5$. Fig. 59a, b, young complete shell viewed dorsally and ventrally, displaying the spinose ornamentation and close fit of the umbones externally. BB63452, $\times 3$. Fig. 60, lateral view of incomplete shell showing part of the spiralia inside. BB63446, $\times 4$. Fig. 61a–c, adult specimen viewed dorsally, ventrally and posteriorly; the ventral umbo is broken, allowing the dorsal umbo to be seen tucked within its cavity. BB63445, $\times 2$.



Figs 62–65 *Cleiothyridina fimbriata* (Phillips). Fig. 62, a stereoscopic pair illustrating the spinose ornamentation on an incomplete ventral valve. BB62975, $\times 2.5$. Fig. 63a, b, internal views looking ventrally and posteriorly in an incomplete young ventral valve, lacking thickening around the dental plates; the cyrtomatodont teeth show, one throwing its typical shadow to the valve floor (arrowed). BB63448, $\times 4.5$. Fig. 64a, b, dorsal and ventral views of juvenile shell. BB63455, $\times 6$. Fig. 65a, b, external and internal views of young ventral valve. BB63453, $\times 5$.

DISCUSSION. The first illustration we have of *C. fimbriata* (Phillips) is that of Davidson (1861: pl. 18, fig. 11). Davidson commonly restored the appearance of the specimens he figured and this is true of this particular illustration, as can be seen by comparing it with his original drawing (vol. 10 of Davidson's drawings in the BM(NH)). This original drawing, annotated by Davidson as being 'in Phillips Collection marked fimbriata No. 202', compares very closely with a specimen in the Phillips collection of the Oxford University Museum (E1093), the specimen designated as lectotype (see Brunton 1980: fig. 19a, b). This Phillips specimen came from 'Florence Court'

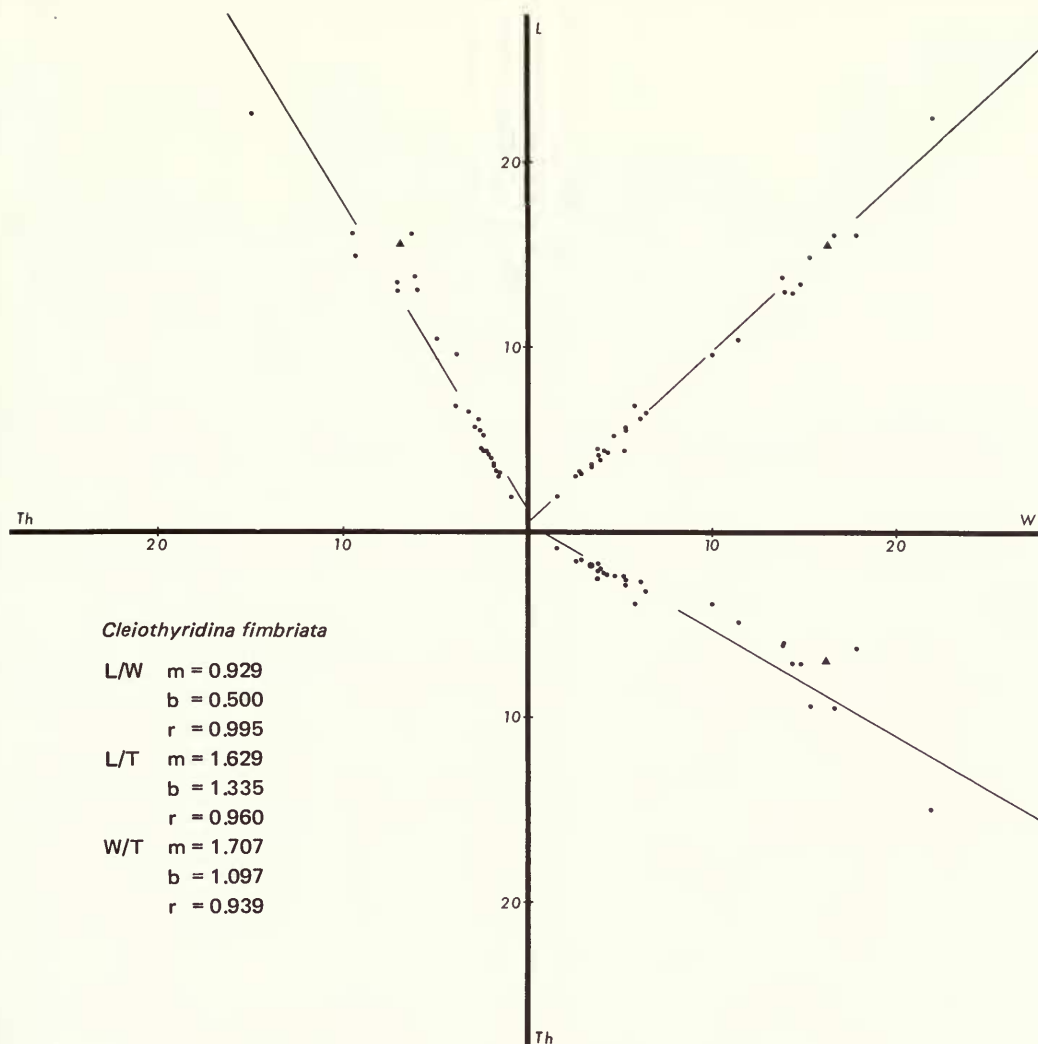


Fig. 66 *Cleiothyridina fimbriata* (Phillips). Length, width and thickness plots of 28 specimens from Co. Fermanagh, plus the lectotype (▲) also from Co. Fermanagh. m = slope of regression line; b = intersection point of m with the axis; r = coefficient of correlation.

(Phillips 1836: 220) in Co. Fermanagh, about 13 miles SSE of the main collecting locality for the silicified material described here. The actual locality of the specimen is unknown, but it is likely that it was collected from the well-exposed Glencar limestones and shales of the Cladagh river, about 3 miles west of Florence Court. In all known respects the specimen is conspecific with the sample population described here.

Since the publication of Davidson's (1861) fine illustrations of this species, unfortunately misidentified as *C. deroissyi* (Léveillé), the name *fimbriata* has largely gone out of use. George (1932), believing there was no foundation for the species and that *S. fimbriata* Phillips was probably a *Reticularia* sp. close to *R. imbricata* (Sowerby), argued that the 'name be discarded'. If it were not for Davidson's good, if somewhat embellished, illustration of the type specimen, which still exists, this would be a sensible suggestion. But in view of the above facts and the need to return to Léveillé's original concept of *S. deroissyi*, the author follows Ramsbottom (1969: 10) in retaining Phillips' species. Thus Phillips' name *fimbriata* is here used to describe specimens

hitherto commonly named as *deroissyi* and often cited incorrectly as being the type species of *Cleiothyridina*.

The most striking feature of *C. fimbriata* is its spinose external ornamentation (Fig. 62). During ontogeny these spine-like structures increased in both girth and length. On larger shells (20 to 25 mm long) there are at least 50 to 60 growth lines from which the spinose lamellae extended, at least during the life time of the animal (Davidson 1861: 85 records up to 80 of these lamellae). More rapid shell growth during early ontogeny resulted in more widely spaced growth lamellae on the umbonal regions than anteriorly. This wider spacing, together with the maximum time for abrasion during life, results in the umbones normally being bald. The best 'spines' were developed late in life, and anteriorly individual 'spines' measure about 0.3 mm in width close to their base, and taper very gradually for a length of at least 5 mm. In the silicified material these largest 'spines' are hollow, but this may be a silicification phenomenon and remains to be demonstrated in unaltered specimens.

Rare variants occur in which the spine-like processes are very fine (c. 0.1 mm wide) and thus less well differentiated from the intervening extremely delicate shelly lamella, which seems to be composed of a single layer of long secondary shell fibres. At present there is no evidence that this variation is other than intraspecific.

The orientation of the spinose lamellae altered during ontogeny and differs with respect to the two valve surfaces. On ventral valves the lamellae and 'spines' extend at a more or less constant low angle from the external valve surface so that at the anterior margin of adult shells the 'spines' project anterodorsally. On the dorsal valve these lamellae project from the surface at an increasingly higher angle from the umbo to the anterior margin where the 'spines' also project anterodorsally, parallel to those of the ventral valve. They did not, therefore, interlock around the commissure when the shell was closed, but formed a closely fitting flange or corona extending from the valve margins.

FUNCTIONAL MORPHOLOGY. These brachiopods were pedunculate, attached to the substrate by a thin pedicle which probably 'rooted' into sediment rather than onto hard fragments of detritus or pebbles. None of the silicified specimens shows signs of umbonal distortion or undue abrasion (Figs 54, 59), as commonly occurs on specimens attached to hard surfaces by a pedicle. The spinose lamellae formed marginal flanges throughout ontogeny and probably helped in the maintenance of a sediment-free brachial cavity, in a fashion similar to that postulated by Shiells (1968) for *Kochiproductus*.

In rare instances there is evidence, from silicified material in which the external ornamentation is preserved posteriorly, of the degree to which these shells could have opened. In such shells the lamellae lateral to the umbones are sparsely developed, especially on the ventral valve (Fig. 61a, c). This relatively smooth area is that over which the dorsal valve moved, as the shell opened, and indicates a gape of up to about 20°. This compares with gape angles of about 15° and 20° respectively for dead shells of the Recent *Hemithyris psittacea* (Gmelin) and *Terebratella dorsata* (Gmelin). The teeth and sockets are relatively open anteriorly but the teeth are typically cyrtomatodont (Jaanusson 1971), being recurved posteriorly as a result of posterior resorption of the previously-developed shell material of the teeth (Fig. 63b). As Jaanusson (1971) stated, these posteromedially-protruding, hook-shaped teeth are typical of Rhynchonellida. Spiriferida and Terebratulida, tended to hold the two valves strongly together and limited the degree to which the shell could open. In *C. fimbriata*, and other athyridaceans, posterior resorption of the teeth was necessary to allow the dorsal umbo free movement into the ventral umbo when the shell opened.

RANGE. *C. fimbriata* is known from Lower Carboniferous rocks throughout the British Isles, but seems not to have extended far into Europe. Closely related species occur in the Lower Carboniferous of Russia, the Elburz, Iran (e.g. *C. kusbassica* Besnossova 1963) and in the south-western states of the U.S.A. (e.g. *C. glenparkensis* Weller or *C. sublamellosa* (Hall)).

In the British Isles the species ranges through late Tournaisian and Viséan strata and the related species mentioned above from Russia and North America are found in rocks mostly equivalent in age to Tournaisian. The species may be found in argillaceous limestones, as in the

silicified Fermanagh faunas, shales or, less commonly, associated with the so-called 'reef' limestones. It seems to have tolerated a soft sea floor composed of fine silt to mud grade sediment. In the silicified faunas it occurs about twice as commonly as *C. deroissyi* and with a larger proportion of young shells.

Cleiothyridina deroissyi (Léveillé)

Figs 67–73

- 1835 *Spirifer De Roissyi* Léveillé: 39; pl. 2, figs 18–20.
 1843 *Terebratula Royssii* (Léveillé) de Koninck (*pars*): 300; pl. 21, figs 1a?, 1b–d.
 1851 *Terebratula squamigera* de Koninck: 667; pl. 56, figs 9a–d.
 1887 *Athyris Roissyi* (Léveillé) de Koninck: 85; pl. 19, figs 28, 29.
 1887 *Athyris squamigera* de Koninck: 82; pl. 20, figs 16–22.
 ? 1914 *Cleiothyridina prouti* (Swallow); Weller: 474; pl. 79, figs 13–16.

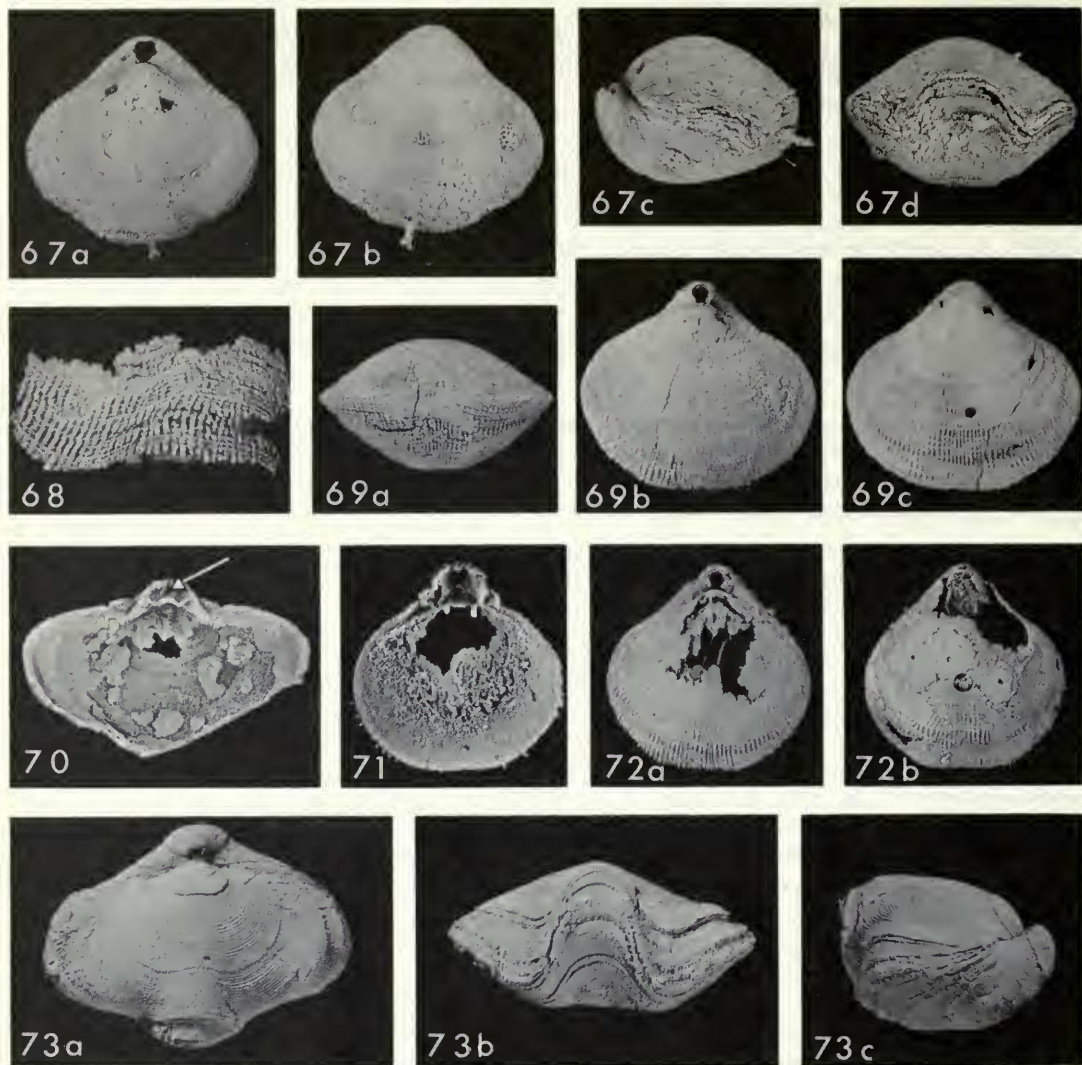
DIAGNOSIS (emended). Circular (young) to transversely elliptical in outline, strongly biconvex shells. Dorsal fold and ventral sulcus persistent, forming strong parasulcate anterior commissure. External ornamentation of closely-spaced growth lines from which extend radially-arranged spinose lamellae, which, when preserved, form a dense mat.

NEOTYPE. Léveillé's specimens appear to be lost. A lectotype of *A. squamigera* de Koninck has been selected (Brunton 1980: 229), which is thought to be conspecific with *deroissyi*. This specimen is here selected neotype of *Spirifer deroissyi* Léveillé.

DESCRIPTION. Adult shells are unusually transverse for the genus and, with a thickness exceeding half the shell width, are thicker than *C. fimbriata*. The strong parasulcate anterior commissure results from a fold and sulcus which persisted throughout ontogeny (Fig. 67d). Both umbones are incurved, the dorsal being tucked below the ventral umbo, in which is a circular pedicle foramen opening anteriorly to the wide delthyrium bordered by low ridges (Fig. 69b). There is no true interarea, but on larger shells the posterior margin of the ventral valve may be flattened as a result of the movement of the valves against each other as the shell opened and closed.

The external ornamentation developed throughout ontogeny, but is normally fully preserved only towards the margins of the valves. Short lamellose growth lines developed at regular and frequent intervals (about 5–7 per mm) throughout ontogeny, from which grew radially-aligned, flattened, spine-like projections, commonly giving the growth lines a serrated appearance (Fig. 69). When fully developed these outgrowths formed a dense 'mat' in which the 'pile' lay oblique to the valve surface and formed an extension to the valve margins (Fig. 68). For the two sets of spinose lamellae to meet parallel to each other at the anterior commissure, those of the ventral valve projected at an increasingly high angle from the valve surface during ontogeny. On large specimens the lamellae are subparallel to the ventral valve surface posteriorly, but may be perpendicular to the surface near the anterior margin. The mat-like pile appears to have originated close to the valve surfaces from the shelly fibres, which constitute the lamellae, separating laterally from median bundles of fibres. These formed the distally diminishing spinose elements of the lamellae. In this way spinosity is lost distally and the valve surface appears to be covered by a dense needle-like pile. On the silicified Fermanagh specimens normally only the radially-arranged spinose lamellae remain (Fig. 72). It is not known whether the lack of complete ornamentation results from abrasion prior to silicification, non-silicification of the needle-like pile, or loss of this structure during acid development. However, a combination of the first two is suspected.

The ventral valve is furnished with slightly hooked cyrtomatodont teeth supported by short dental plates, which do not extend anteriorly from the umbonal cavity, except immediately below the teeth. The intersection of the tooth and supporting plate is marked posteriorly by a narrowly triangular shelf just below the margins of the delthyrium, a region in which some resorption of the teeth must have taken place during ontogeny. The paired adductor scars are more or less elliptical in outline, close to the mid-line and sunk below the internal shell surface. The diductor scars are poorly differentiated and have not been clearly distinguished.



Figs 67–73 *Cleiothyridina deroissyi* (Léveillé). Fig. 67a–d, complete shell viewed dorsally, ventrally, laterally and anteriorly. BB63461, $\times 2$. Fig. 68, fragment of a ventral valve with well-preserved ornamentation. BB63466, $\times 4$. Fig. 69a–c, young shell viewed anteriorly, dorsally and ventrally; the radially-aligned spinose lamellae can be seen, and the ventral valve is bored medially. BB63462, $\times 2.5$. Fig. 70, dorsal valve interior, looking posterodorsally to show the cardinal process, foramen (arrowed), and sockets. BB63464, $\times 2.5$. Fig. 71, juvenile dorsal valve interior with teeth and umbo of the ventral valve remaining attached; the crura extend from the edge of the hinge plate. BB63465, $\times 6$. Fig. 71a, b, incomplete young shell viewed dorsally and ventrally; the ventral valve is bored medially. BB63463, $\times 3$. Fig. 73a–c, adult shell from the Tournai region of Belgium, viewed dorsally, anteriorly and laterally. BM(NH) 65002, $\times 1$.

The cardinalia are not heavily calcified and seem to vary quite considerably in absolute and relative size compared to the valve width. There is insufficient material to allow a full study of this feature, but in two Belgian specimens of about 17 mm and 20 mm width the cardinalia measure 3.5 mm and 5.0 mm respectively, between the bases of the inner socket ridges. The largest Fermanagh dorsal valve is 15 mm wide with cardinalia 5 mm wide. The cardinalia width is obviously linked to the distance between the teeth and the width of the delthyrium. The crural

bases, hinge plates and foramen are illustrated in Fig. 70, in which it can be seen that the cardinal process is much smaller than that of *C. fimbriata*, and it may be that the diductor muscles were unusually slight, leaving little trace in either valve. The dorsal adductor scars are broadly elliptical in outline, separated medially by a low ridge and are slightly sunken. Otherwise the valve interiors are smooth.

DISCUSSION. In the acid-developed Fermanagh faunas there are 30 reasonably complete shells and valves of *C. deroissyi* (about half the number of *C. fimbriata* specimens).

C. fimbriata differs from *C. deroissyi* (Léveillé) both externally and internally. The most obvious differences are shell shape and ornamentation; *C. deroissyi* is a more transverse shell than *C. fimbriata*; it is thicker and the anterior commissure is strongly uniplicate as a result of a fold and sulcus, both of which originated close to the umbones.

The pedicle foramen is large and the umbones less incurved than in *C. fimbriata*. The external ornamentation contrasts with that of *C. fimbriata* in being much finer; growth lines are ill-defined, close together and regularly spaced and from them extend short, radially aligned, spinose lamellae. As in *C. fimbriata* the spinosity increases anteriorly, but never on *C. deroissyi* are long discrete spines preserved. The cardinalia of *C. deroissyi* differ in having a low cardinal process and gently arched conjoined inner hinge plates, with a large triangular foramen posteriorly.

The nomenclatorial history of *C. deroissyi* (Léveillé) is vexed. The original description (1835) is brief, but the three illustrations are characteristic in all respects, save for a lack of information upon the external ornamentation. De Koninck (1843) described and figured specimens under this name, some of which agree with Léveillé's description, others of which should probably have been referred to *C. fimbriata* (pl. 21, figs 1g, h). Subsequently (1851, 1887) de Koninck called *fimbriata*-like specimens *deroissyi* and put up a new name, *squamigera*, for specimens which should have been called *deroissyi* Léveillé. Davidson (1861) perpetuated the name *deroissyi* for specimens of *C. fimbriata* (Phillips). This incorrect use of the name *deroissyi* for a distinctive and fairly common western European athyridacean led to its adoption as the type species of *Cleiothyridina*, a course which has been challenged for many years by the Russians and more recently by Carter (1967), and which is here corrected (p. 57). Within the collections of the BM(NH) are specimens from de Koninck's collection named '*Terebratula squamigera* de Kon.' in his own handwriting (Fig. 73). These, and several other specimens from the Tournai area of Belgium, are relatively wider and thicker compared to their length than are the Fermanagh shells, but in other respects, such as details of ornamentation, cardinalia and articulation, they appear to be identical. From the growth lines on the Belgian shells it is clear that the length: width ratio remained fairly constant during ontogeny. The width of these shells did not, therefore, result from allometric growth in which width exceeded length only late in ontogeny. This partially silicified Belgian material is probably of Tu2 (C₁) age; the Fermanagh specimens are judged to be Viséan (Asbian, D₁ ≡ V3b). A Tournaisian specimen from the Bristol area is like the Belgian specimens in shape and it may be that the species became relatively narrower, thinner and less sulcate during the Carboniferous.

The large athyridaceans from Belgium, reaching about 35 mm in length, are perhaps referable to *Athyris ingens* de Koninck (1887: 83); they appear to be a group of brachiopods showing characteristics intermediate between those of *C. deroissyi* and *C. fimbriata*. The external ornamentation is essentially *fimbriata*-like, and the size of the shell is more in keeping with this species. The strongly uniplicate anterior commissure is more reminiscent of *deroissyi*, but this folding only developed at about half the full valve length, and it could be argued that had *C. fimbriata* shells grown to this size they might have become similarly folded. Should this prove to have been the case, *C. ingens* should be considered as a large variant of *C. fimbriata*. It may be that the rare large specimens illustrated by Davidson (1861: pl. 18, figs 1-4) as '*A. Royssii*' (more correctly *C. glabristria* (Phillips)) should belong in this group, and that *C. glabristria* is a *C. ingens* stripped of its external ornamentation.

The pedicle foramen seems to have remained relatively large and accessible throughout ontogeny and it may be that this species relied upon its pedicle attachment to the substrate to a

greater extent than did *C. fimbriata*. The small cardinal process myophore and indistinct ventral valve diductor muscle scars may indicate relatively long, thin diductor muscles, or a diductor system requiring less muscular energy to operate than in other thinner-shelled species, or both.

RANGE. *C. deroissyi* (Léveillé) occurs relatively commonly in the Tournaisian of Belgium but rarely in rocks of similar age in the British Isles. The species extends up through the mid-Viséan in Britain. *C. prouti* (Swallow) is a closely similar species from the Tournaisian (Fern Glen) of the south-western U.S.A.

Family **NUCLEOSPIRIDAE** Davidson 1881

Genus **NUCLEOSPIRA** Hall 1859

TYPE SPECIES. *Spirifer ventricosus* Hall 1857 from the Devonian Lower Helderberg group of New York State.

DISCUSSION. The genus is seldom recorded from Lower Carboniferous rocks, other than those of the Mississippi valley, U.S.A., where it appears to be confined to rock of Tournaisian age. The genus reappears in uppermost Mississippian rocks (= Namurian) of Montana, U.S.A.

Nucleospira carlukensis (Davidson)

Figs 74, 76–82

v* 1859 *Spirifera carlukensis* Davidson: 59; pl. 13, figs 14, 14a, b.

not 1863 *Spirifera carlukensis* Davidson: pl. 55, figs 14, 15.

DIAGNOSIS. *Nucleospira* with slight median sulcation on ventral valve, anterior commissure weakly uniplicate. Microspinous external ornamentation on both valves. Large tapering cardinal process with bifid tip curving posteroventrally into ventral valve umbo. Median ridges in both valves low.

LECTOTYPE. *Spirifera carlukensis* Davidson, Davidson collection figured 1859: pl. 13, figs 14, BM(NH) B7627, here selected as Lectotype. From the Hosie Limestone (late Viséan) of Hillhead, near Carluke, Lanarkshire (Fig. 77).

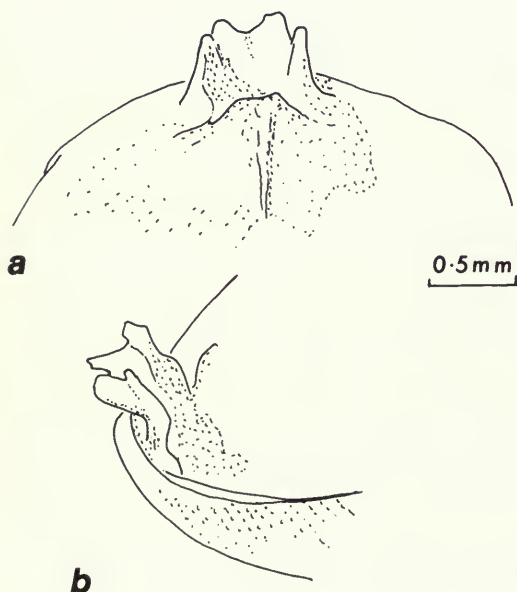


Fig. 74 Drawings of the cardinalia of *Nucleospira carlukensis* viewed (a) posterodorsally and (b) laterally, to show the large hooked cardinal process. (See also Fig. 80a, c).

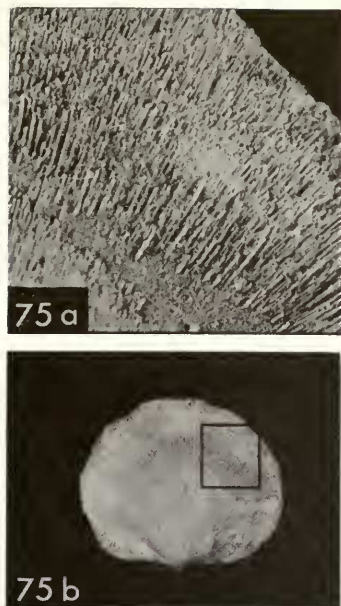
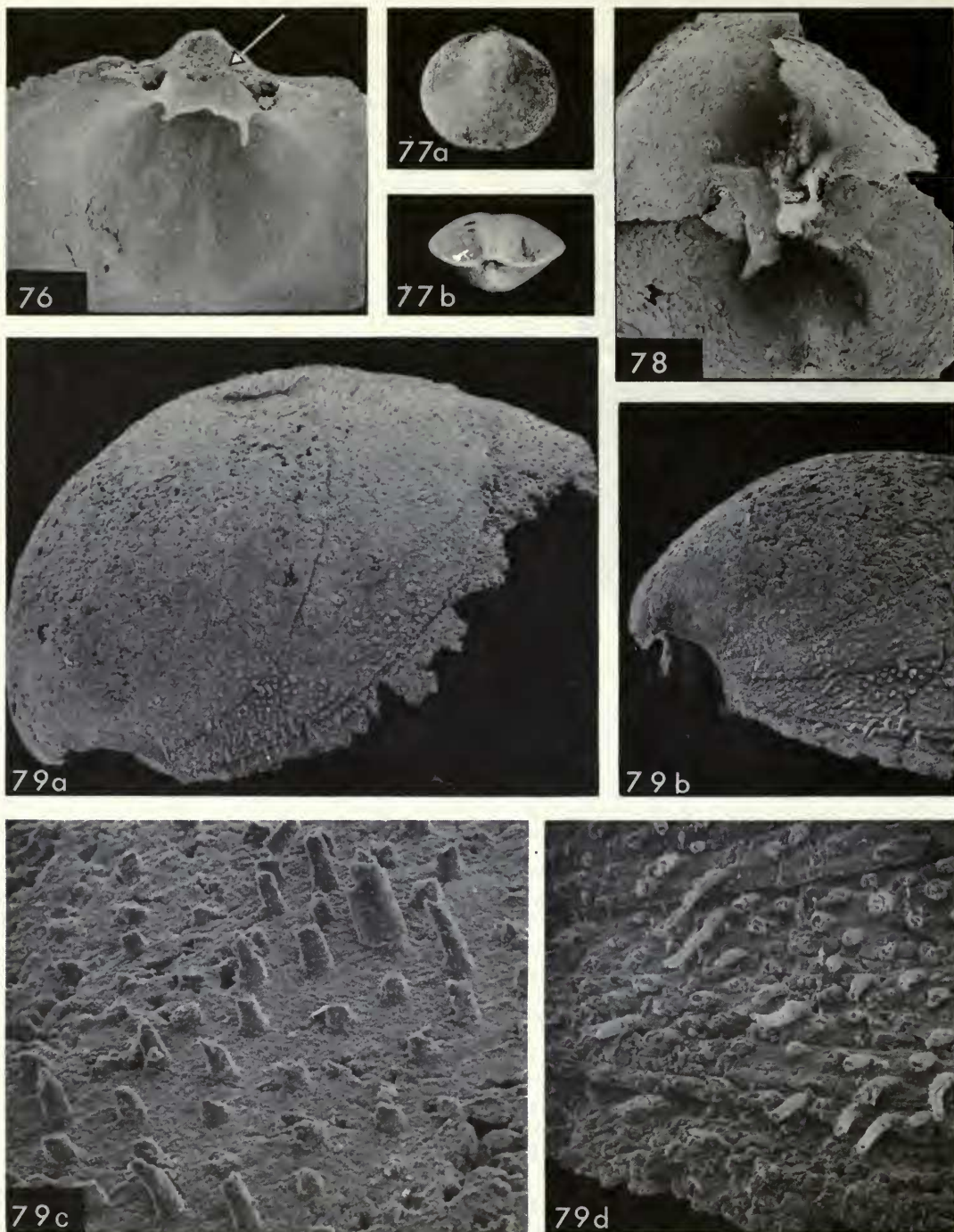


Fig. 75 The external microspinosose ornamentation on the dorsal valve of *Nucleospira concinna* Hall, from the mid-Devonian of Wadsworth, New York, U.S.A. BB19736, (a) $\times 10$, (b) $\times 1.5$.

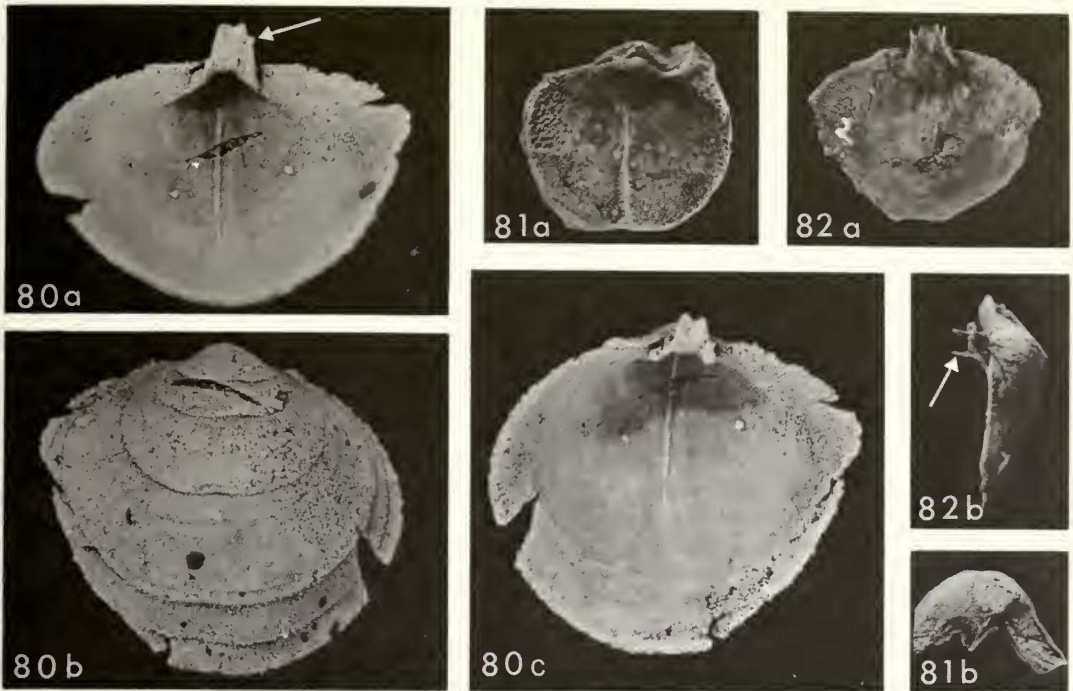
DESCRIPTION. The species is small (commonly about 5 mm wide, but reaching about 10 mm wide), circular to transversely broadly elliptical in outline and equibiconvex in profile. The hinge line is 2.0 to 2.5 mm wide in shells 5–8 mm wide. The ventral interarea is apsacline, slightly concave and with an open, relatively wide delthyrium. The dorsal umbo is prominent, but an interarea is lacking. The ventral valve commonly has a shallow median sulcus forming a weakly uniplicate anterior commissure. Both valves are ornamented with irregularly, but commonly anteriorly concentrated, growth lines and concentrically arranged fine spines of irregular diameter (Brunton 1976: pl. 115). The spines project radially, at high angles from the valve surfaces, with a frequency of 15–20 spines per mm measured along a growth band; they have not been observed more than about 0.3 mm in length (Fig. 79). The teeth are short and crytomatodont in character. There are no dental plates but the delthyrial margins are thickened (Fig. 81a). A low median ridge extends from the umbonal cavity nearly to the anterior margin, posteriorly dividing the weakly-impressed muscle scars; the adductor scars are elliptical in outline, restricted to the umbonal cavity and enclosed laterally and anteriorly by wide diductor scars which may extend for nearly one-third of the valve's length.

The dorsal valve interior is typified by the ventroposteriorly-projecting, hook-like cardinal process (Fig. 80). The sockets are small and the differentiation between the inner socket ridges, flanks of the cardinal process and crural bases is poor (Fig. 74). The floor of the socket curves ventrally without interruption, to form the crural base and flank of the cardinal process. The crura extend anteroventrally about midway between the socket and tip of the cardinal process (Figs 78, 82), which is bifid. The cardinal process is concave posteroventrally and its external (posterior) surface effectively seals the delthyrial opening; the myophores are situated distally on the ventrally- to ventroposteriorly-facing surfaces. Thus, with the exception of the crura, the whole cardinalia played a direct role in the articulation of the shell (Fig. 78), the teeth articulated against the posterolateral surfaces of a structure combining the functions of inner socket ridges and cardinal process base. A low median ridge extends from the dorsal umbonal cavity for at least half the valve's length. The adductor scars are narrowly ovate and positioned posteriorly adjacent to the median ridge; from their anterior margins extend the raised impressions of the 'vascula media'.

DISCUSSION. In 1859 Davidson utilized two spellings for this species: the plate explanation (and labels on his specimens in the British Museum (Natural History)) being spelt '*carlukiensis*'. The



Figs 76–79 *Nucleospira carlukensis* (Davidson). Fig. 76, internal view of the posterior region of a ventral valve, in the delthyrium of which is fitted the cardinalia: their broken surface is arrowed and the crura project above the muscle scars on the valve floor. BD113, S.E.M. $\times 25$. Fig. 77a, b, **lectotype** (herein selected), from the late Viséan near Carluke, Lanarkshire, viewed ventrally and posterodorsally. B7627, $\times 4$. Fig. 78, pair of slightly crushed umbo interiors. The dorsal valve (uppermost) shows the left socket and half the cardinal process curving ventrally towards the ventral umbo; the cardinal process and other socket are broken in the whiter areas. BD115, $\times 25$. Fig. 79a–d, ventral valve in lateral and slightly posterolateral views showing the interarea, delthyrium and some of the microspinous ornamentation, with details of the microspines anteromedially and posterolaterally. BB61625, S.E.M. (a) $\times 25$, (b) $\times 40$, (c), (d) $\times 150$.



Figs 80–82 *Nucleospira carlukensis* (Davidson). Fig. 80a–c, dorsal valve viewed posterodorsally, externally and dorsally, to show the external ornamentation and internally, the cardinal process with its lateral crural bases and the median ridge. BB63458, $\times 6$. Fig. 81a, b, incomplete ventral valve viewed ventrally and posteriorly; the left side of the delthyrium and the tooth have been broken, but the thickened dental ridges and low median ridge are clear. BB63460, $\times 7$. Fig. 82a, b, dorsal valve, interior and posterolateral view; the cardinalia are well preserved with paired projecting crura (arrowed) and posteriorly recurved cardinal process. BB63459, $\times 7$.

name is derived from the Lanarkshire town of Carluke, so should be without the 'i' as it first appeared in print (1859: 59); this is the spelling utilized here.

Davidson thought this small rounded species was related to the similar *Crurithyris urei*, but noted that *N. carlukensis* is equally biconvex whilst *C. urei* is strongly ventri-biconvex. Five specimens are attached to the card in the BM(NH) collections with Davidson's handwritten label marked 'Sp. Carlukiensis'. Of these, two are *Crurithyris* species; from the remaining three the lectotype (B7627) has been chosen. It is probably the specimen figured by Davidson (1859: pl. 13, figs 14), but as two specimens are virtually identical it is impossible to be sure. Davidson noted that his species occurred near Carluke in association with the much commoner *C. urei*. This too is true in the silicified Co. Fermanagh faunas.

In 1863 Davidson illustrated (pl. 55, figs 14, 15) more specimens named 'Spirifera carluikiensis', this time from Narrowdale, Staffordshire. These range in width from 7 to 12.5 mm but otherwise bear external similarity to the type specimens. Their shell is partially exfoliated exposing a coarsely fibrous secondary shell structure, the fibres being up to about 0.03 mm wide. This contrasts with the very fine secondary fibres of the Carluke specimens and reinforces the doubt as to these two forms being conspecific; the Narrowdale specimens are possibly young specimens of *Coledium*.

The number of specimens of *N. carlukensis* recovered from the Fermanagh limestone is relatively small, there being about 50 reasonably preserved valves, including valves down to 1.4 mm wide. Even in these smallest valves the dorsal cardinalia are relatively large and neither the shell shape nor the internal morphology altered to any marked extent during ontogeny, other than by size increase. Variation within the assemblage can be recognized in details of the

cardinalia, some of which taper distally more rapidly than others, leading to a narrow and almost pointed tip, contrasting with the more normal wide bifid tip. It is to be expected that this characteristic would correlate with the width and length of the delthyrium, into which the exterior surface of the cardinal process fits. Unfortunately, however, there are insufficient associated dorsal and ventral valves to allow direct observation of this feature.

The rarity and small size of these brachiopods probably accounts for their absence from the British literature. *Nucleospira* species have been described from the well-preserved Mississippian shale faunas of North America, and species such as *N. barrisi* White and *N. minima* Weller appear to be very similar to *N. carlukensis*, the latter especially so in size. These species are found in rocks of about mid to upper Tournaisian age. A third species, *N. superata* Easton from the Cameron Creek Formation of Montana, is very similar externally to *N. carlukensis*, but the important characteristics of the cardinalia were not described (Easton 1962). The age of the Cameron Creek Formation is uncertain, but Easton suggests that his *Nucleospira* species is of Chester age, the age commonly accepted for the underlying Heath shales. If this is correct, *N. superata* is slightly younger than *N. carlukensis* from northern Britain. Neither the reviewed European nor Russian literature records *Nucleospira* species and, judged by the published faunal illustrations, the genus would not seem to be present under a different name.

If the paucity of *Nucleospira* species and specimens is genuine, rather than collecting failure, it may be that the present distribution can be explained as that of a migrating group of species, close to the limits of their environment, undergoing allopatric (geographical) speciation; the distribution would be from North America, where the group is well represented in the Devonian, to Britain by mid to upper Viséan time, and becoming confined to northern and central North America by the uppermost Mississippian.

Superfamily CYRTIACEA Frederiks 1919 (1924)

Family AMBOCOELIIDAE George 1931

Genus *CRURITHYRIS* George 1931

TYPE SPECIES. *Spirifer urei* Fleming 1828: 376 (as figured by Ure 1793: pl. 14, fig. 12), by original designation of George 1931: 43. Lectotype selected by George (1931: pl. 4, figs 1a–d), Ure Collection, Hunterian Museum, Glasgow (L1790), from high D zone, Viséan of Strathaven, Lanarkshire, Scotland.

DESCRIPTION. Strongly ventribiconvex Ambocoeliidae with hinge line less than width of shell. Commonly with microspinose external ornamentation. Cardinal process sessile to low with ridged to tuberculate myophore, adductor scars commonly enclosed posteriorly by crural bases and extending anteriorly up to two-thirds of valve length. Dental plates lacking.

DISCUSSION. Additional information about the valve interiors necessitates a revision of the diagnosis. It is suspected that all *Crurithyris* species were originally spinose externally and that it is simply lack of preservation which has led to the reporting of smooth species. A form of spinose ornamentation can often be recognized on well-preserved shale specimens and upon many finely silicified specimens. Material cracked from limestone has commonly lost its external shell because the ornamentation clings to the surrounding rock.

The genus is widely distributed in high Devonian through to low Permian strata. It appears not to have persisted into the Carboniferous of Australia, although known from the upper Devonian of Western Australia. The Givetian species *C. jurkowicensis* Balinski 1973, from the Holy Cross Mountains, Poland, might be placed more appropriately in the genus *Ambocoelia*.

Crurithyris urei (Fleming)

Figs 83, 85–92

1793 [un-named] Ure: pl. 14, fig. 12.

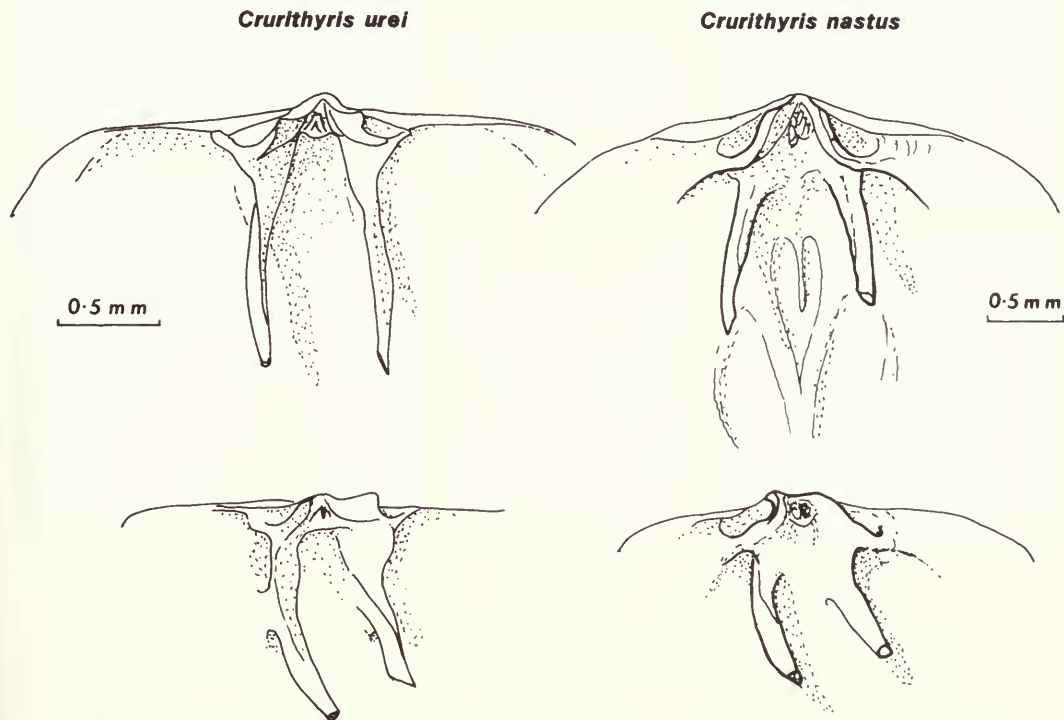
v* 1828 *Spirifer urei* Fleming: 376; specimen figured by Ure.

- 1859 *Spirifera urei* (Fleming); Davidson: 58 (*pars*); ? pl. 12, figs 14.
 ? 1899 *Ambocoelia parva* Weller: 20; pl. 4, figs 1-4.
 1931 *Crurithyris urei* (Fleming) George: 55; pl. 4, figs 1-4.
 v. 1931 *Crurithyris magnispina* George: 50; pl. 5, figs 1-4.

DIAGNOSIS. Small, anteriorly weakly sulcate *Crurithyris*; exterior with fine growth lines, ornamentation of small and minute spines with or without superficial radial grooves. Dorsal adductor scars anterior to pedicle adjustor scars, placed between widely-spaced subparallel crura. Ventral valve lacking median ridge.

LECTOTYPE. *Spirifer urei* Fleming, Ure Collection, Hunterian Museum, Glasgow (L1790). Selected by George (1931: 55).

DESCRIPTION. Small ventribiconvex shells with an apsacline ventral interarea and very short catacline dorsal interarea. The dorsal umbo is slight and both valves are weakly sulcate anteriorly. Growth lines are very fine, commonly ill-defined or more clearly developed only anteriorly. The external surface is pitted by minute cavities, arranged more or less concentrically with a frequency of 15 to 20 per mm width, from which extend minute spinose projections in exceptionally well-preserved specimens. A set of larger spinose projections occurs on ventral valves with a spacing of 0.1 to 0.2 mm (Figs 92b, c). Teeth are small, semi-oval in outline and project a little medially of the margin of the delthyrium, which is bordered by narrow deltidial plates and internally by low dental ridges (Figs 88b, c, 89). Ventral muscle scars are lightly impressed, the adductors being confined umbonally and more or less narrowly obovate in outline. The diductor scars appear to be widely spread from the anterolateral margins of the adductors. A ridge of secondary shell bounds the delthyrial apex internally and confines the posterior ends of the muscle scars. Within the dorsal valve the cardinal process is a small



Figs 83-84 Drawings of the dorsal valve interiors of *Crurithyris urei* and *C. nastus*, to illustrate differences in the inner socket ridges and crural bases. The upper two drawings are viewed dorsally, the lower two obliquely.

tuberculate or weakly longitudinally ridged area raised on the short notothyrial platform situated within the apex of the inner socket ridges (Fig. 90b). While the sockets themselves are shallow the inner socket ridges are prominent, especially anteriorly, so as to articulate strongly with the teeth. Crural bases support the sockets and extend dorsomedially to fuse with the valve floor posteriorly. There are no inner hinge plates. The crura are subparallel and extend about two-thirds of the dorsal valve length before curving ventrolaterally (Fig. 90) into the ribbon of the three-coiled spiralia. The posterior pair of adductor scars are slightly sunken, elliptical in outline and extend anteriorly from between the crural bases. The anterior adductor muscle scars are commonly less well defined and flank the posterior scars anterolaterally. Their outline and position is variable but generally they are somewhat reniform, tending to enclose the anterior margins of the posterior scars; they trail posteriorly to the crural bases. The complete adductor field is divided medially by a low ridge. Apically, between the crural bases there are indistinct pedicle adductor muscle scars.

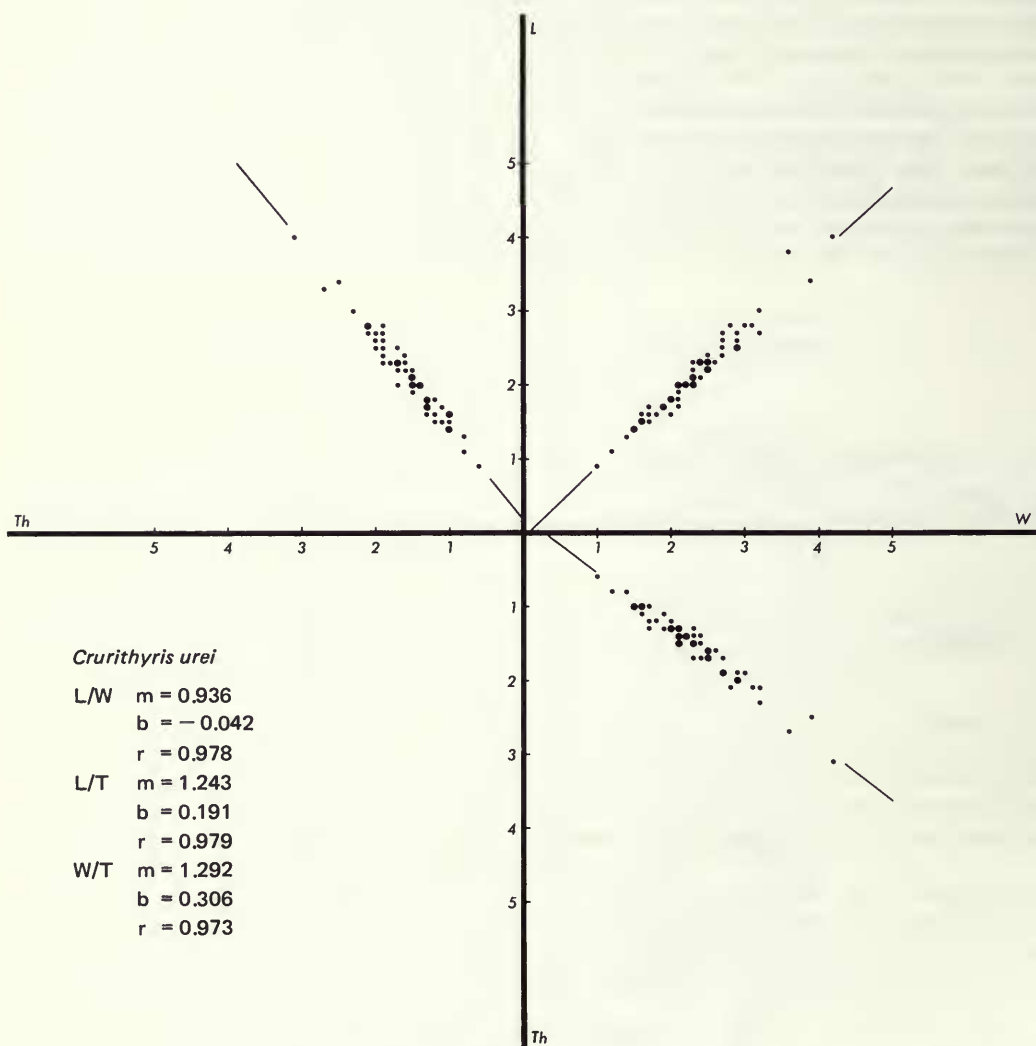
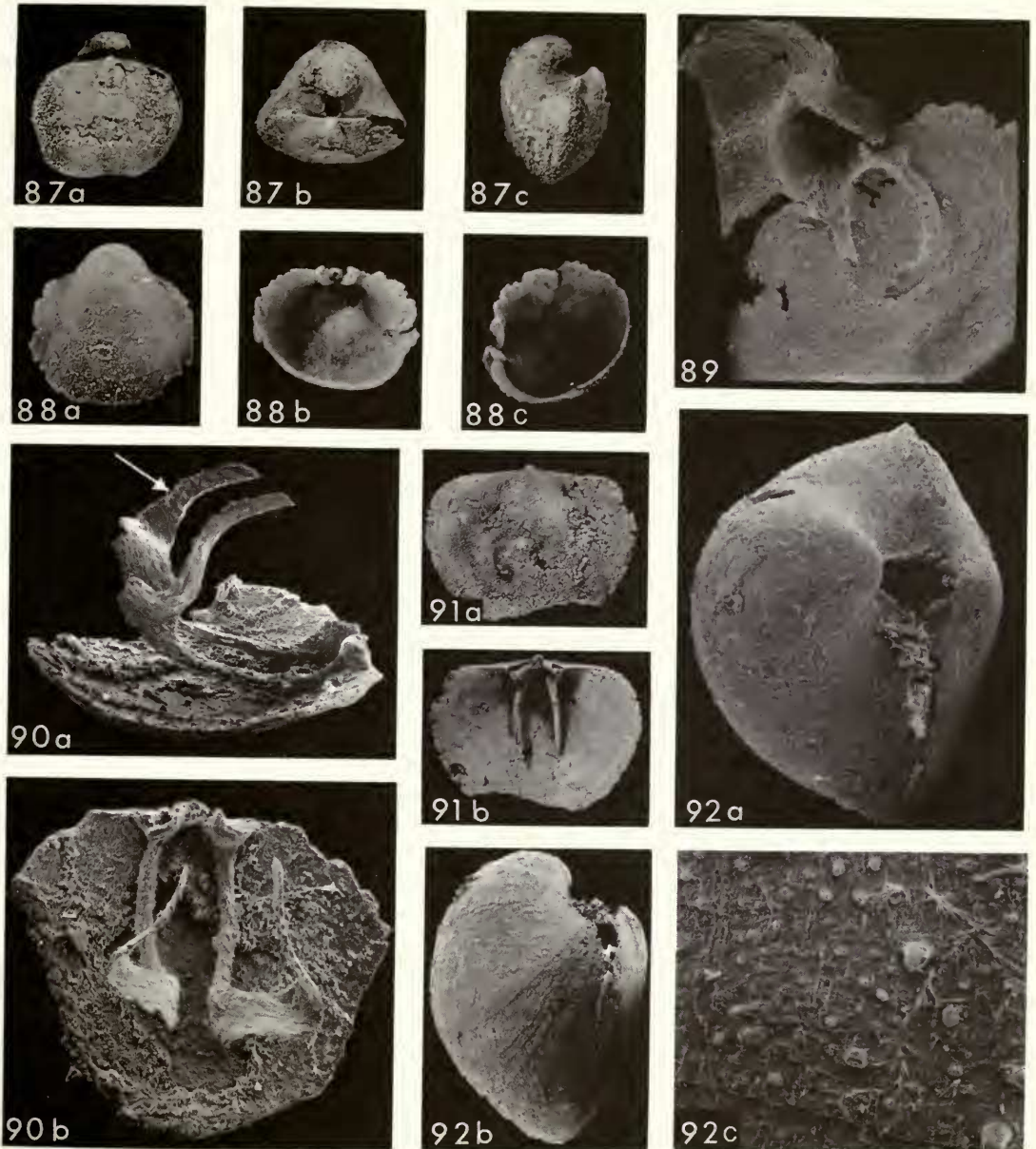


Fig. 85 *Crurithyris urei* (Fleming). Length, width and thickness plots of 60 specimens from Co. Fermanagh. m = slope of regression line; b = intersection point of m with axis; r = coefficient of correlation.



Figs 86–92 *Crurithyris urei* (Fleming). Fig. 86, stereoscopic pair illustrating the interior of a shell, showing the cardinalia and crura. BB63457, $\times 5$. Fig. 87a–c, dorsal, posterior and lateral views of complete adult shell. BB63551, $\times 5$. Fig. 88a–c, external and internal posterior and oblique lateral views of a ventral valve showing the microspinosus ornamentation, the teeth and dental ridges. BB63456, $\times 8$. Fig. 89, dorsal valve with articulated ventral valve umbo, viewed internally to show the articulation, dental ridges and crura. BD1170 (broken), S.E.M. $\times 28$. Fig. 90a, b, dorsal valve with complete crura and start of the spirallium viewed laterally and dorsally; note the nodose anterior edge at the start of the spirallium (arrowed) and prominent inner socket ridges. BD150, $\times 20$. Fig. 91a, b, adult dorsal valve exterior and interior. BB63552, $\times 6$. Fig. 92a–c, posterior and lateral views of a complete shell, with detail of the microspinosus ornamentation on the anterolateral margin of the ventral valve. BB61624, S.E.M. $\times 20$, $\times 15$ and $\times 75$, respectively.

DISCUSSION. The species is common in the Fermanagh silicified faunas, there being in excess of 500 specimens, but the individuals are small, seldom reaching more than 4 mm in length (Fig. 85). The lectotype is 4.3 mm long and Ure's largest specimen is 4.8 mm long (from George 1931). Like *C. parva* (Weller), as shown by Carter (1967), *C. urei* changed little in its relative dimensions during ontogeny. Curvature of the valves is most marked posteriorly so that the young dorsal valve is relatively more convex than that of adult shells, which like the ventral valve becomes relatively flattened anteriorly.

The spinose external ornamentation is very fine, yet was noted by Davidson in 1859 and illustrated by him in 1863 (pl. 54, fig. 14). George (1931) described this feature in some detail and utilized the presence of two sizes of 'spines' on both valves as a characteristic of his new species *C. magnispina*; he considered all the Davidson (1859, 1863) figures, called *S. urei*, as illustrating his new species. However, George noted that 'in certain forms the larger spines occur only on the anterior and lateral portions of the dorsal valve, the umbonal region being only microspinous'. Thus, only in fully grown specimens of this large species, reaching about 9 mm in length, were the characteristic big 'spines' seen on dorsal valves. On smaller specimens, at sizes characteristic of *C. urei* (3 to 4 mm long) the spinose arrangement would have been as recorded for *C. urei*. The differentiation of these two species included details of the dorsal adductor muscle scars, disposition of crural bases and overall size, features which appear to have varied sufficiently within themselves to allow a continuous gradation and indeed overlap between the two species, which here are considered synonymous.

Crurithyris fissa George, from the D₂ zone 'reefal' limestones of Parkhouse Hill, Derbyshire is distinct whilst *C. amoena* George, from the uppermost Viséan of the Gower, is very similar to, and possibly conspecific with, *C. urei*. A large sample of *Crurithyris nastus* Brunton & Champion 1974, collected by Mr C. Champion in the Manifold valley from rocks probably of early Viséan, Chadian age, superficially resembles *C. urei* but differs in having a distinctly striated cardinal process, less well developed, or posteriorly differentiated, crural bases, and a low median ridge in both valves (see Figs 83, 84).

The spinose external ornamentation is only preserved in some shale specimens and acid-developed silicified material. Both the smaller and larger 'spines' are arranged in ill-defined concentric bands but the larger 'spines' are less regular in their occurrence. All seem to be solid, but as George (1931: 37) suggested, it seems probable that while close to the valve margin these spines were tubular, their inner surfaces being lined with secretory epithelium. The minute cavities marking the positions of abraded spines indicate that the epithelium probably plugged the spine end with calcite and then atrophied. The epithelial evaginations would have been pinched off from the outer mantle epithelium and secondary shell secreted over the inner ends of the cavities, which project slightly into the shell looking a little like a very fine endopunctuation, as seen from the valve exterior. On rare specimens small grooves about 0.2 mm in length extend anteriorly from some of the 'spine' bases. These grooves probably represent the refusion of the mantle epithelium, and consequently of the primary shell layer, at the distal (marginal) side of the spine, following the budding of the generative epithelium responsible for the growth of the spine (see Brunton, 1976).

The dorsal musculature for *Crurithyris* presented by George (1931: fig. 3b) is based upon an internal mould of his species *C. amoena* (also figured 1931: pl. 5, fig. 6) and as such is an overgeneralization of the situation. Although it is true that the dorsal muscle field is generally confined within the anteriorly-extended lines of the crural bases, the adductor muscle scars themselves are variably positioned and shaped. It could be argued that the posterior scars are positioned between the crural bases and that the anterior pair of adductor scars is subdivided. Alternatively, and more likely, all the adductor scars are positioned level with or anterior to the anterior ends of the crural bases and the small indistinct scars distinguishable posteriorly, close to the base of the cardinal process, are those of pedicle adjustor muscles. The anteriormost position of adductor muscle scars is about two-thirds of the dorsal valve length (in a valve only 2.6 mm long). This rather more anterior grouping of the adductor muscle scars in *C. urei* places them in an intermediate position between George's (1931) fig. 3 'A' and 'B', 'A' being a representation of the dorsal valve interior of *Ambocoelia*. In separating *Crurithyris* from

Ambocoelia Hall, 1860, George stressed differences in the dorsal musculature and cardinal process. In fully-developed specimens of *A. umbonata* (Conrad), the type species, the cardinal process is weakly striated in much the same way as in some larger *Crurithyris* species. The dorsal musculature of the type species of both genera are more similar than suggested by George and their classification together in his family group Ambocoeliidae is satisfactory. It may be that mid-Devonian *Ambocoelia* species evolved via the Manifold valley *Crurithyris* forms to the high Viséan *C. urei* and *C. fissa*.

RANGE. *Crurithyris urei* (Fleming) is typical of high Viséan rocks in northern Britain. A similar but distinct species, *C. nastus*, occurs in older rocks probably of low Viséan age in the Derbyshire–Staffordshire area, and the similar species *C. amoena* occurs in high Viséan rocks of south Wales. Well-authenticated occurrences of *C. urei* are lacking from western Europe, but it is recorded from high Viséan and less commonly down to Tournaisian strata of the Moscow basin (Sarycheva & Sokolskaya 1952). Aizenverg (1966, 1971) figures the species from Tournaisian strata in the Donetz Basin, but from the illustrations this record seems doubtful. Neither the species nor any closely comparable have been described from the Viséan of Australia. Weller's (1899) Tournaisian species, *Crurithyris parva* from the south-western U.S.A., is similar to *C. urei*, but is placed in synonymy with considerable doubt!

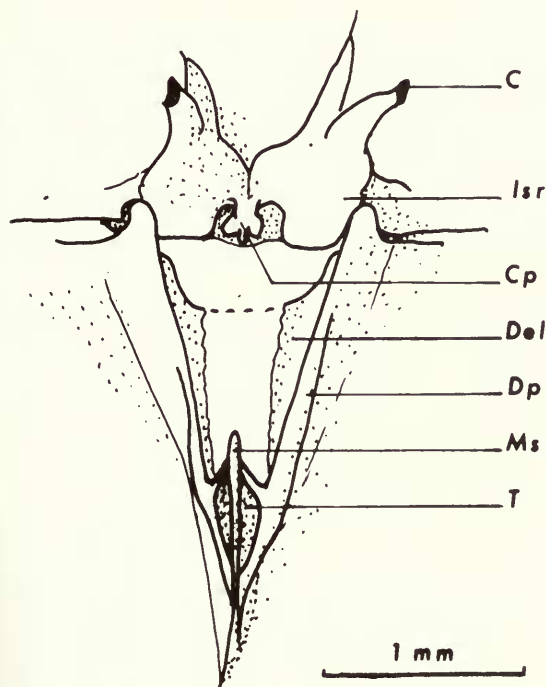


Fig. 93 Drawing of the internal umbral structures of *Cyrtina hibernica* sp. nov. (see Figs 101, 102). The dorsal valve is uppermost. C = crura; Isr = inner socket ridge, articulating with a tooth laterally; Cp = cardinal process; Del = deltidial plate; in adulthood, these met medially as a complete cover; Dp = dental plate, descending to fuse with the median septum Ms; T = tichorhinum, developed as a pair of chambers, one each side of the median septum.

Superfamily SUESSIACEA Waagen 1883

Family CYRTINIDAE Frederiks 1912

Genus CYRTINA Davidson 1859

TYPE SPECIES. *Calceola heteroclita* Defrance 1828: 306, by subsequent designation of Miller (1889: 342) – see Anderson, Boucot & Johnson (1969).

DISCUSSION. The genus was well described by Davidson (1858: 66), Hall & Clarke (1894: 43) and Weller (1914: 286). The type species is from mid-Devonian strata and it was at that time that the genus appears to have been most prolific. The generic name has been used for British Lower

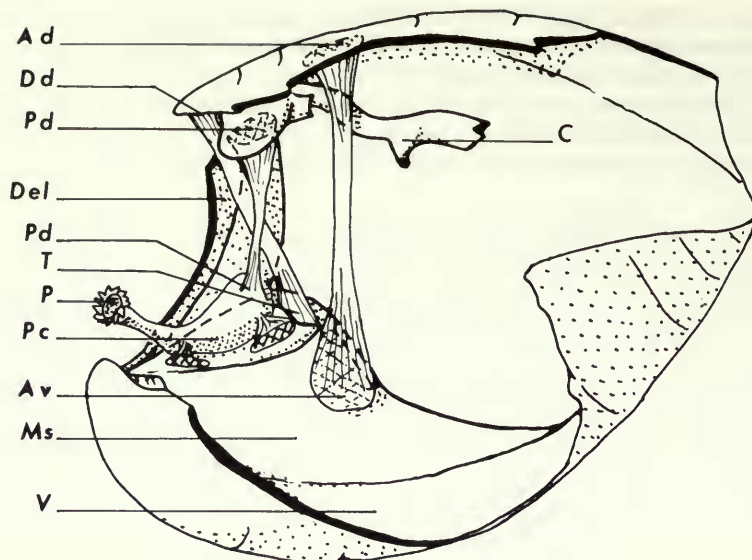


Fig. 94 Diagrammatical reconstruction of the musculature of *Cyrtina hibernica* sp. nov., viewed laterally. C = crura, with the stump of the jugum; Ad = dorsal adductor muscle scar; Dd = dorsal diductor muscle point of attachment, the cardinal process; Pd = dorsal attachment, on the inner socket ridge, of the pedicle adjustor muscle, with its origin from the pedicle capsule, Pc; Del = part of the delthyrial cover; T = tichorhinum, accommodating the ventral ends of the diductor muscles; P = the distal end of the pedicle; Pc = pedicle capsule, from the ventrolateral margin of which extend short adjustor muscles attached to the inner surfaces of the dental plates; Av = ventral attachment area of the adductor muscle; Ms = posteriorly high median septum, accommodating the muscle; V = floor of the ventral valve.

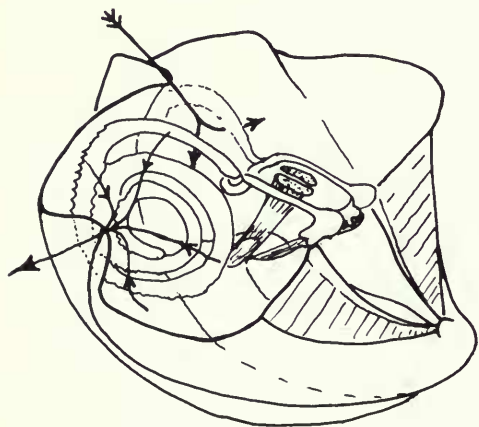


Fig. 95 Diagrammatical reconstruction of *Cyrtina hibernica* sp. nov., showing the inferred feeding/respiratory flow of water through the spiralia. The dorsal valve is drawn as transparent, to show the left spirulum and the adductor and diductor muscles.

Carboniferous species, such as *C. septosa* (Phillips), *C. dorsata* (M'Coy) and *C. carbonaria* (M'Coy), but these species are now placed in *Davidsonina* Schuchert & Le Vene 1929, leaving no well-known *Cyrtina* species in the Carboniferous. However, Davidson (1863: pl. 52, fig. 15) has illustrated a *Cyrtina* species, which he called *Spiriferina insculpta* (Phillips), from the Lower Scar Limestone of Settle. The whereabouts of this specimen is unknown but within Davidson's unfigured collection in the BM(NH) there are three conspecific specimens from the Wetton district of Staffordshire (B5416), also called *Spiriferina insculpta* by Davidson (ms label). The Fermanagh specimens are the first British Carboniferous *Cyrtina* species to be named, within the modern concept of the genus.

Cyrtina hibernica sp. nov.

Figs 93–107

? 1863 *Spiriferina insculpta* (Phillips); Davidson: pl. 52, fig. 15.? 1974 *Cyrtina* cf. *burlingtonensis* Rowley; Brunton & Champion: pl. 110, figs 17–19.1976 *Cyrtina* sp.; Brunton: pl. 115, fig. 7.

DIAGNOSIS. Small *Cyrtina* reaching nearly 8.00 mm wide with three prominent dorsal and four ventral ribs. External ornamentation finely papillose to microspinose. Ventral median septum prominent posterior to tichorhinum, below deltidial plates.

MATERIAL. The species is common from both the collecting localities but most are figured from the Silles river locality.

HOLOTYPE. BB63704 from the Silles river locality (Fig. 97).

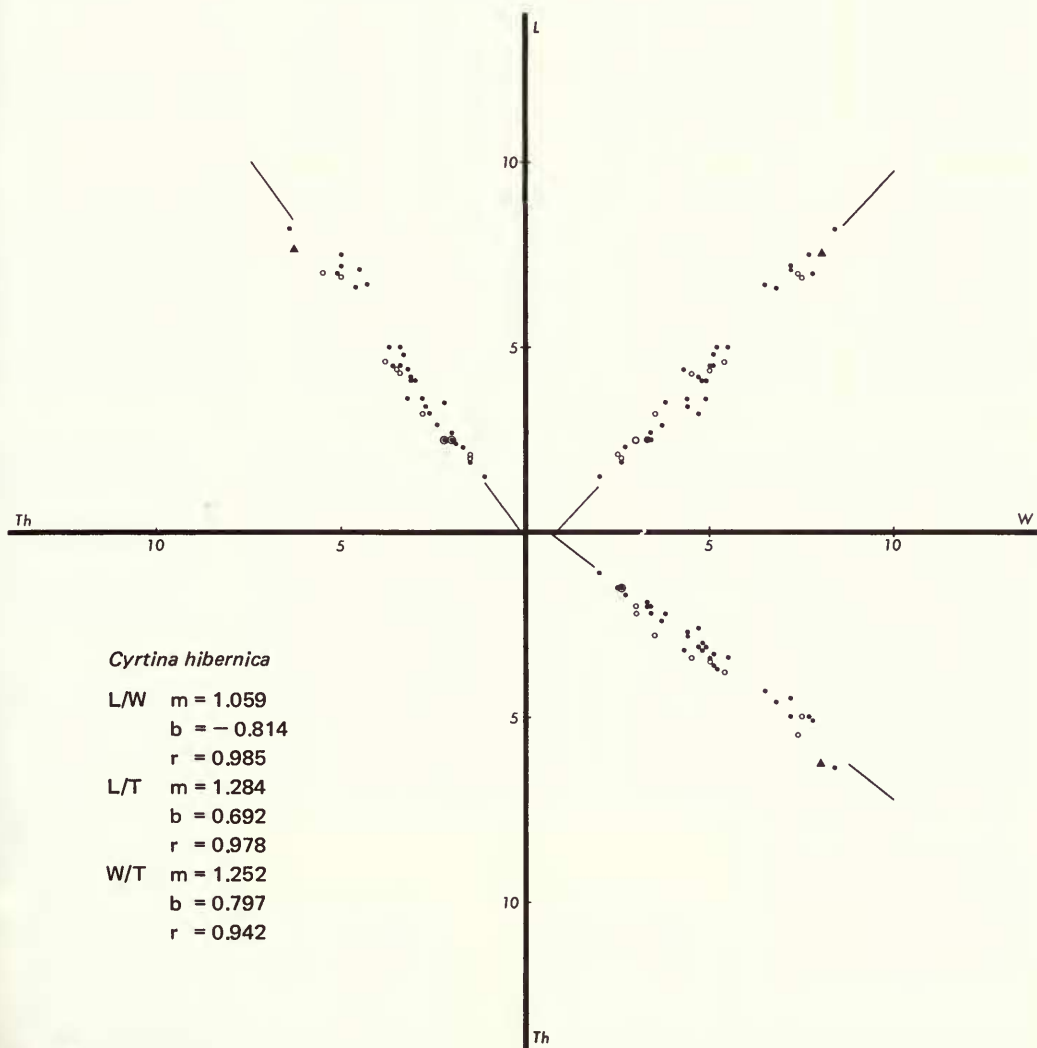
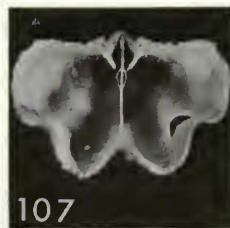
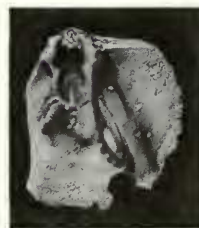
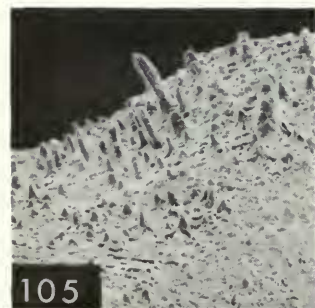
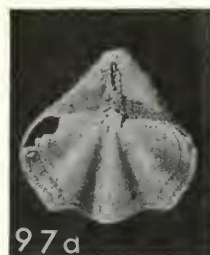


Fig. 96 *Cyrtina hibernica* sp. nov. Length, width and thickness plots of 30 specimens from the Silles river locality (●) and 10 specimens from the Carrick Lough locality (○); the holotype is differentiated (▲). m = slope of regression line; b = intersection point of m with axis; r = coefficient of correlation.



DESCRIPTION. The outlines of this species are typically cyrtiniform, but in lateral profile the ventral interarea is always apsacline. The external ornamentation is of few prominent ribs, the ventral median sulcus and dorsal median rib originating at the umbones, and the additional pair of ribs on each valve starting within the first 1 mm of growth. Growth lines are developed sporadically and external surfaces are ornamented by minute papillations and true microspines (Fig. 105). The delthyrial covering is variably developed; deltidial plates arch the delthyrium, especially dorsally (Fig. 101), and may fuse leaving a posteroventral narrowly ovate pedicle aperture (Fig. 97a).

The ventral valve has short, rounded, knob-like teeth (Fig. 103) supported by dental ridges which extend ventrally into the dental plates, forming a spondylium-like structure raised high from the floor of the valve by the median septum (Fig. 101b). The posterior edge of the median septum forms a conspicuous plate-like ridge along the 'spondylium' from the umbo to beyond its dorsal extremity. The tichorhinum is divided by the median septum and is supported posteriorly by the dental plates (Figs 101a, 102). The dorsal edge of the median septum is almost perpendicular to its posterior edge within the 'spondylium'. Dorsally concave, arcuate, low ridges on the median septum are growth features, possibly associated with muscle scars. Adult dorsal valve interiors have short, laterally tapering, flat interareas bordering shallow sockets (Fig. 104). The internal socket ridges are high blade-like structures providing the main articulatory surfaces (Figs 99, 103); they diverge from the umbo at approximately 90° from one another, but towards their anterior margins they tend to recurve posterolaterally. The adult cardinal process is normally bilobed with longitudinally striated myophores (Fig. 98a). The bases of the socket ridges, together with the crural bases, form what is almost an anteroventrally-directed concave sessile cardinal plate. The dorsal pedicle adjustor muscles probably attached to this area, at the bases of the crura (Fig. 98a). The crura extend anteriorly, following the positions of the sulci bordering the median rib. At a length of about 0.6 mm a ventroposterior prong from each crus bends anteriorly to fuse medially as a complete jugum (Fig. 106). There is a short, anterodorsally-projecting median process which, together with the jugum, is tuberculate on its anterior surface. The brachial axis is directed slightly posteroventrally of laterally and each spire seems to have had no more than three coils, each of which is strongly fimbriate anteriorly. On the floor of the dorsal valve indistinct low ridges border the adductor muscle scars medially and laterally.

ONTOGENY. From the Silles river locality the proportions of complete shells to disarticulated valves is about 100 shells to 150 ventral valves and 110 dorsal valves. The total numbers recovered from both localities are about twice these figures. The size range of the specimens is from 1.5 mm wide to 8.0 mm wide (Fig. 96), allowing excellent opportunity for ontogenetic study and a more complete description of internal structures than has been possible hitherto.

Figs 97–107 *Cyrtina hibernica* sp. nov., from Co. Fermanagh. Fig. 97a–d, **holotype** viewed dorsoposteriorly, dorsally, ventro-anteriorly and laterally; note the incomplete delthyrial cover. BB63704, $\times 3$. Fig. 98a–c, a dorsal valve viewed respectively internally, showing details of the cardinalia (crural base arrowed) $\times 15$, and internally complete $\times 5$, and externally $\times 5$. BB63709. Fig. 99, dorsal valve interior with part of the first coil of the spiralia preserved; Carrick Lough locality. BB63823, $\times 5$. Fig. 100a, b, young shell viewed posterodorsally, showing the incomplete delthyrial covering (arrowed), and dorsally; Carrick Lough locality. BB63824, $\times 3$. Fig. 101a–c, a ventral valve viewed posterodorsally and dorsally showing the relationships of the 'spondylium', tichorhinum (arrowed) and deltidial plates ($\times 4$), and viewed externally ($\times 3$). BB63705. Fig. 102, internal structures (tichorhinum arrowed) of an incomplete but articulated shell. BD109, S.E.M. $\times 12$. Fig. 103, cardinalia and articulation of an incomplete, but articulated, shell. BD107, S.E.M. $\times 8$. Fig. 104, internal view of a mature dorsal valve showing the cardinal process, strong internal socket ridges and large crural bases. BB63708, $\times 5$. Fig. 105, margin of ventral valve showing the external microspinose ornamentation. BB61627, S.E.M. $\times 50$. Fig. 106, stereoscopic pair of photographs of dorsal valve interior showing jugum and first loop of spirulum, with its nodose anterior edge; Carrick Lough locality. BB63822, $\times 7$. Fig. 107, internal (ventral) view of an immature ventral valve; there is a circular bore-hole towards the margin on the right hand side. BB63706, $\times 5$.

Even in the smallest ventral valves the median septum is conspicuous protruding apically into the delthyrial opening. The 'spondylium' and tichorhinum are not developed. At a shell width of 2.00 mm the dental plates are just distinguishable and fuse to the median septum forming a rudimentary tichorhinum. The cardinal process is minute and the jugum arises from the crura at about half the dorsal valve length, i.e. at about 0.8 mm from the dorsal umbo. By a shell width of 3.00 mm the 'spondylium' and tichorhinum are well developed, the former extending to about one-third of the length of the delthyrium, the margins of which are already arched by rudimentary deltidial plates. The cardinal process is a distinct knob-like structure, the inner socket plates are well developed but the position of the jugum is still at nearly half the dorsal valve length. Thereafter growth continued regularly, except that the cardinal process commonly became bilobed by a shell width of 4.00 mm, and the degree of growth of the deltidial plates varied. From the available material it seems that the development of a complete deltidium in adults was unusual. As all stages between well-separated and fused deltidial plates can be observed the term deltidium is appropriate. However, the median line of junction cannot be seen on the deltidium and were it not for the evidence from other specimens this structure would be termed a pseudodeltidium. *Cyrtina* is normally defined as having a pseudodeltidium, but in terms of growth it seems likely that other *Cyrtina* species also possess deltidia developed as in *C. hibernica*.

Within the dorsal valve anterior migration of the jugum (accompanied by resorption along its posterior edge) did not keep pace with the anterior growth of the primary lamella. Thus, by adulthood (valve length of about 4.00 mm) the jugum is only 1.5 mm from the dorsal umbo; it remains at this position during further growth of the shell.

DISCUSSION. The relationship of *C. hibernica* with certain other *Cyrtina* species is reasonably clear. It is most closely related to *C. burlingtonensis* Rowley, originally described from the base of the Burlington Limestone, Missouri, U.S.A. The species has since been described from other formations in the U.S.A. of Kinderhook or low Osage age (= Tournaisian). The two species differ in that *hibernica* always has three dorsal and four ventral ribs, compared to the five and six of *burlingtonensis*; the 'spondylium' is deeper, within which the median septum is higher, and it would seem that the deltidial cover is less well developed in *hibernica*. Brunton & Champion (1974) described two specimens from possible Chadian to early Arundian rocks near Wetton, Staffordshire, as *C. cf. burlingtonensis*. These two specimens are very similar to *C. hibernica* and should perhaps be included here. However, the complete specimen from Wetton shows faint additional ribs laterally and so approaches *C. burlingtonensis* in this feature. Considering its stratigraphical position, the Wetton form may be considered as an intermediate. There is a clear trend from the Devonian species, *C. heteroclita*, to this new species in which the ribs are reduced in number and the differentiation of the median fold and sulcus reduced in prominence. The cardinal angles (from the interarea to the ventral valve flank) change from acute to rounded and the delthyrial covering appears to have been reduced during evolution from Devonian through the Lower Carboniferous.

FUNCTIONAL MORPHOLOGY. The unusual structure of the tichorhinum has led to speculation upon the muscle system of *Cyrtina*. Within the dorsal valve the situation is quite clear; diductor muscle attachment to the posteriorly-facing myophores of the cardinal process, and adductors attached medially between the crura and dorsal pedicle adjustor muscles, which attached onto the crural bases (bases of the inner socket ridges; Fig. 93). In the ventral valve it has been agreed generally that the high median septum provided areas of attachment for muscles. In the *Treatise* (Williams *et al.* 1965) Williams & Rowell would have both the diductor and adductor muscles attached to the median septum and the base of the pedicle housed within the tichorhinum. In his study of spiriferide shell structures MacKinnon (1974) recognized myotest on the flanks of the median septum and within the base of the tichorhinum of a Devonian *Cyrtina* species. He interpreted the tichorhinum as accommodating the adductor muscle bases and the diductor muscle attachment as being on the median septum anteriorly. This muscle arrangement is close to that of Recent articulate brachiopods and is that which perhaps provides the most mechanically sound system within shells the shape of *C. hibernica*. The pedicle and pedicle capsule would have been within

the delthyrial cavity and covered, to a variable extent, by the deltidial plates. The ventral pedicle adjustor muscles were probably attached within the 'spondylium', on either side of the median ridge, and the dorsal adjustors to the bases of the inner socket ridges (Fig. 94). Such an arrangement poses the problem that the adductor and diductor muscles must have crossed one another, close to the anterodorsal margin of the median septum, all very close to the median plane of the shell. In order to overcome this problem the muscles must have been very narrow and tendinous. An alternative arrangement, less analogous to Recent brachiopods, is for the adductor muscles to have been attached to the median septum below the tichorhinum, and for the diductor muscles to have been seated in the tichorhinum. In this situation the dental plate–median septum structure would have been a true spondylium in that it would have accommodated the adductor and diductor muscle bases, the former being separated from the latter by the tichorhinum (Figs 93, 94).

RANGE. *C. hibernica* is a common fossil from the sampled rocks at the Silles river and Carrick Lough localities. It has been found also at a point about one mile NNW of the Silles locality, on the Milltown Bridge stream, in *Schellwienella*-rich argillaceous limestone of the Glencar Formation. This position would suggest an age slightly older than the main fauna under description. If the Manifold valley *Cyrtina* specimens are conspecific then the species may have its origin low in the Viséan. In western Europe *Cyrtina* species appear to be uncommon but forms intermediate in external characteristics between *C. heteroclita* and *C. hibernica* are known from the Tournai region of Belgium. Closely similar species are not recorded from Lower Carboniferous rocks of Russia. A single specimen of a similar, but relatively wider, species has been recorded from the Utting Calcarene (mid-Viséan) of the Bonaparte Gulf Basin, Australia (Roberts 1971).

Superfamily **SPIRIFERACEA** King 1846

Family **DELTHYRIDIDAE** Waagen 1883

Subfamily **TYLOTHYRIDINAE** Carter 1972

Carter (1972) proposed this subfamily for 'lamellose Delthyrididae with variable outline and moderately numerous lateral costae; micro-ornament apparently lacking; interior of pedicle valve with high median septum and dental adminicula; brachial valve lacking tabellae'. Besides *Tylothyris* North, he included *Texathyris* Carter 1972, a low to mid-Tournaisian genus from Texas. At family level Carter distinguished the Delthyrididae from the Mucrospiriferidae principally on the presence of a ventral median septum in the former, a characteristic carried through to the subfamily and genus *Tylothyris*. The Tylothyridinae was differentiated from the family group by its lack of the fimbriate micro-ornament typical of Delthyrididae.

Genus **TYLOTHYRIS** North 1920

TYPE SPECIES. *Spirifer laminosa* M'Coy 1841, by original designation of North (1920), from Hook Head, Co. Wexford, Ireland.

Tylothyris laminosa (M'Coy)

Figs 108–119

1841 *Spirifer laminosa* M'Coy: 26.

1844 *Cyrtia laminosa* (M'Coy) M'Coy: 137; pl. 21, fig. 4.

1858 *Spirifera laminosa* (M'Coy); Davidson: 36 (*pars*); pl. 7, figs 17–20.

1887 *Spirifera laminosa* (M'Coy); de Koninck: 103 (*pars*); pl. 22, figs 44–50; pl. 30, figs 30, 31.

v* 1920 *Tylothyris laminosa* (M'Coy) North: 197; pl. 13, fig. 16.

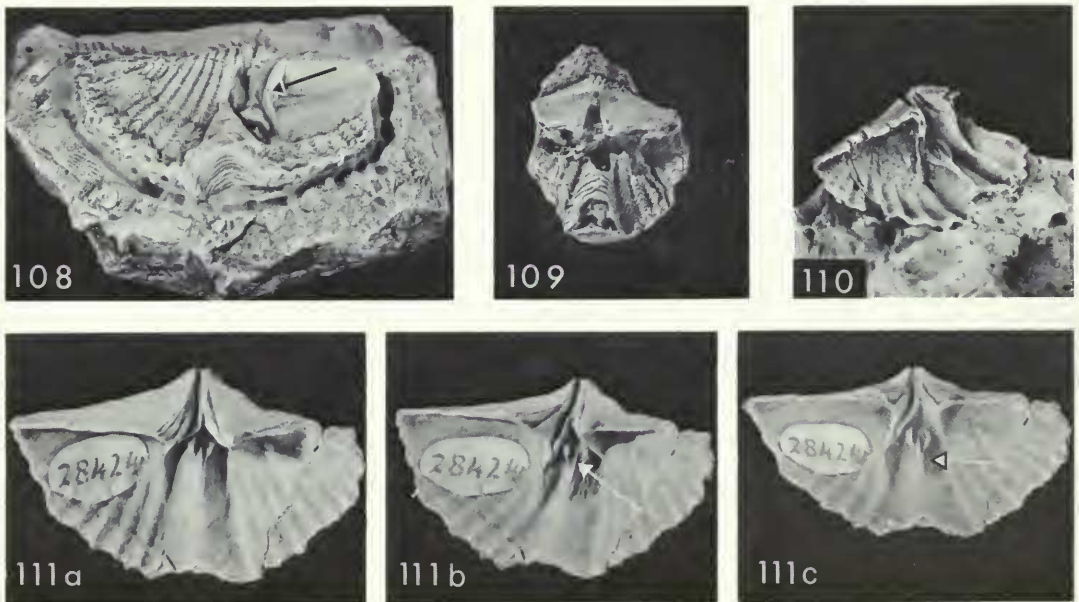
1920 *Tylothyris laminosa*, mut. γ North: 200; pl. 13, figs 1, 2, 12, 13.

DIAGNOSIS. Transverse *Tylothyris* with concave long ventral interarea and delthyrial angle commonly about 35°; externally convex incomplete delthyrial cover. Nine or ten simple costae on either side of prominent fold and sulcus; entire, regular lamellose growth lines. Dental plates

recurved posteriorly to floor of valve and buried posteriorly in apical callosity. Small, raised, narrowly ovate adductor scars separated by low median septum extending nearly half valve length.

NEOTYPE. Contrary to previous designations, M'Coy's species dates from 1841 when, in a descriptive appendix to his catalogue of the Museum of the Geological Society of Dublin, he described the species in the same way as in his better known 'Synopsis' of 1844. There was no figure in 1841, but M'Coy did state that the species was found at 'Hook' (Hook Head, Co. Wexford). The collections of the Society were handed over to Trinity College, Dublin, in 1848, but unfortunately searches there have failed to discover any *Cyrtia laminosa* specimens from the Geological Society, so no lectotype can be selected.

In his redescription of the species North (1920: 198) designated as 'Holotype' a dorsal valve from Hook Head, Co. Wexford, housed in the British Geological Survey, Leeds (IGS 28425; Fig. 108). There is no evidence that this specimen was ever in M'Coy's possession, or in the collection of Griffith, which formed the basis of M'Coy's 1844 'Synopsis', when he repeated his 1841 description. There are eight known Griffith Collection specimens in the National Museum of Ireland, Dublin, labelled as '*Cyrtina laminosa* M'Coy'; they are from Ballinacourty, Co. Waterford, Poulscadden, Co. Dublin (3), Malahide, Co. Dublin (Fig. 109), Ballintrillick, Co. Leitrim (but the village is now in Co. Sligo), and Abbeybeg and Finner, Co. Donegal. None are from Hook Head; the only known Griffith specimens from Hook Head are those in the Sedgwick Museum, Cambridge (E7273 and E7274), both dorsal valve exteriors, and neither of these closely resembles M'Coy's figures (1844: pl. 21).



Figs 108–111 *Tylothyris laminosa* (M'Coy). Fig. 108, the **neotype** selected herein, from Hook Head, Co. Wexford; the dorsal valve has been removed on the right-hand side exposing the dental plates (arrow). Leeds IGS 28425, $\times 1$. Fig. 109, incomplete specimen in the Griffith Collection, National Museum of Ireland, Dublin, from Malahide, Co. Dublin, $\times 1$. Fig. 110, incomplete silicified ventral valve, partially etched from the rock, from Hook Head, Co. Wexford; the internal pitted area, lateral to the thickened dental plates, can be seen. BB56634, $\times 1.5$. Fig. 111a–c, ventral valve interior viewed ventrally, ventrolaterally and ventroposteriorly to show the dispositions of the dental plates, low median septum and raised adductor muscle scars (arrow on Fig. 111b); the diductor muscle scars are arrowed on Fig. 111c. Hook Head, Co. Wexford; IGS 28424, $\times 1.5$.

From M'Coy (1841) and Griffith (1862) it is clear that Hook Head should be the type locality for the species. As no extant Griffith specimen was clearly that figured by M'Coy in 1844, North's specimen (IGS 28425) is here selected as **neotype**.

It is noteworthy that the Griffith Collection was, in all probability, collected by Patrick Ganly, the man responsible for much of the field work leading to the various Richard Griffith geological maps of Ireland published from 1838 (see Archer, 1980).

MATERIAL. Ten Griffith Collection specimens mentioned above, plus one from the Bundoran, Co. Donegal in the Sedgwick Museum (E7272), referred to by North as on tablet 636 (1920: 195). Specimens from other collections include two in the I.G.S., Leeds, and about twenty in the BM(NH), all from Hook Head. From the Fermanagh faunas about thirty reasonably complete shells or valves were recovered, mainly from the Sillee River locality (BB63600–BB63609).

DESCRIPTION. North (1920) provides details of the external morphology and some information about the ventral valve interior. From my observations of topotypic material from Hook Head in the BM(NH) collections, and from the silicified Fermanagh specimens, I disagree with North's description on only a few points. North states that the lateral slopes of both valves are ornamented by ten or twelve costae; my experience is that ten is the common number on adult shells and only on one specimen have I counted twelve. Within the ventral valve the median septum is said to reach nearly to the level of the area at the apex (1920: 196). In young ventral valves (about 8 mm wide) this is not true (Fig. 115) and in older valves the shell thickening buried the median septum apically (Figs 111, 116). In old specimens shell thickening fills the apex of the delthyrial cavity to a level just below the interarea. The median septum extends anteriorly from this callosity well below the level of the interarea, separates the narrowly ovate adductor scars, confined laterally by the thickened bases of the dental plates, and continues anteriorly for about half the valve length (measured parallel to the commissure).

The present silicified material provides information on the internal morphology in addition to that presented by North. The ventral adductor scars are raised on small platforms, the surfaces of which are parallel to the commissural plane (Fig. 111b). As a result of shell thickening only the anterior edges of these muscle platforms remain raised above the valve floor in old age. The diductor muscle scars are indistinct but occupy the flanks of the ventral valve median sulcus and extend slightly beyond the anterior end of the median septum, this is a little over half the total valve length. The disposition of the dental plates differs slightly in the Fermanagh specimens from the Hook Head specimens seen. In the former the anterior edges of the dental plates are strongly concave and do not fully support the anterior edges of the delthyrial margins (Fig. 115). In the Hook Head specimens the dental plates are more fully developed anteriorly, supporting the teeth (Fig. 110). On the lateral flanks of the dental plates, and extending laterally for about half the valve width, the internal surface of the valve is ornamented by a series of shallow pits and irregular ridges (Fig. 118). These areas would appear to be those occupied by the gonocoels within the mantle epithelium.

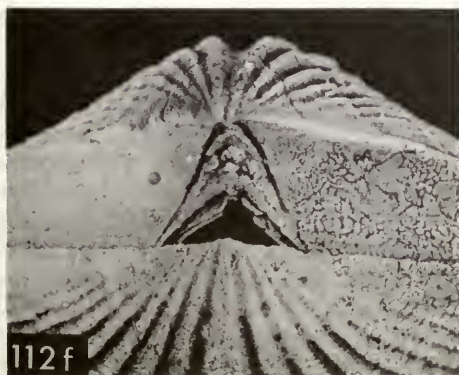
Dorsal valve interiors have not been described previously. The cardinal process is a wide (reaching 2 mm wide in the largest specimens) comblike structure, having deep longitudinal straight grooves (Fig. 114). In detail each ridge is itself ridged so that the ventral face of the myophore, adjacent to the dorsal umbo, has a rough fimbriate appearance. The cardinal process is separated laterally from the inner socket ridges by a shallow groove and is supported dorsally by a median thickened ridge of shell. This ridge narrows on the floor of the valve to divide the ovate adductor muscle scars, which are situated within the depression of the dorsal fold or fastigium (term of Cooper & Grant, 1976). Low ridges of secondary shell surround the muscle scars posterolaterally and, perhaps, provided the sites of attachment for the dorsal adjustor muscles, close to the base of the cardinal process. The sockets originate about ½ mm apart at the dorsal umbo, and extend anterolaterally across the dorsal interarea at about 55° from the mid-line. They are shallow and their floors buttress out from the inner surface of the valve, dorsal of the interarea (Fig. 114). The inner socket ridges are prominent anteriorly, forming a tight fit with the anteromedian faces of the teeth, and merge anteromedially into the crural

bases, which overhang the valve floor about 5 mm apart in the biggest specimens (about 36 mm wide). Neither the jugum nor complete spiralia can be seen in any shell.

ONTOGENY. The smallest ventral valve (4 mm wide) and dorsal valve (7 mm wide) available already show all the internal structures of adulthood. However, in the ventral valve the dental plates are only 0.3 mm long within the umbo (Fig. 113c) and the delthyrial angle is about 30°, as compared to a maximum of 45° in adult valves. The rate of increase in the delthyrial angle reduced during ontogeny, as compared with the total width of the ventral valve. During ontogeny the number of external ribs increased by additions posterolaterally, up to a total on either side of the mid-line of eleven or, exceptionally, twelve. The sulcus originated at the umbo and its anterior width remained about one-quarter of the total width of the shell. The teeth and sockets grew without shell resorption (deltidodont of Jaanusson 1971) and the ventral adductor scars became increasingly bounded posterolaterally by secondary shell deposits. Some of the largest valves are thickened marginally, indicating a continuation of shell deposition despite no further growth in overall size.

DISCUSSION. A delthyrial covering has not been described previously for *Tylothyris*, although North was astute enough to recognize that the grooves bordering the delthyrium indicated the likely presence of a covering structure in life (Fig. 113b). In adulthood the delthyrium is partially closed by an apical shell callosity and a small delthyrial plate. Dorsal to the plate is a series of 3 to 4 triangular stegidial plates, the apical points of which imbricate internally with the previously-formed plate. The dorsolateral margin of the stegidial plates fits onto the groove formed between the edges of the delthyrium and shell thickening on the internal sides of the dental plates (Fig. 112e, f). Similar-looking plates are illustrated in *Gypsospirifer* species, from the Permian of southwest Texas, by Cooper & Grant (1976). What is probably a complete stegidium is preserved on only one specimen (Fig. 112), where a narrow gap remains between its dorsal edge and the cardinal process of the dorsal valve. It seems unlikely that the gap accommodated a pedicle in life since the dorsal ends of the diductor muscles must have occupied part of the space and when the shell was open, for feeding etc., the dorsal valve would have rotated towards the gap. Furthermore, there are no clear signs of adjustor muscle scars on the inner surfaces of the dental plates. It is probable, therefore, that the young were attached by a pedicle but that this atrophied towards adulthood, as the stegidium developed, leaving the adult shell with its posterior surface on, or slightly in, the substrate. A feature which may have aided the stability of these adult shells, but which is seldom preserved intact, is the development along the posterior edge of the valves, at the angles with the interarea, of spinose shelly flanges (Fig. 112a). These grew during life as a result of mantle regression leaving the narrowly pointed ears of the ventral valve as projections extending laterally from the sloping 'shoulders' of the valve. Nalivkin (1976) mentions spines in his essay on the form and function of the interarea in spiriferides, which seem to be the same structures. He, however, interpreted the interarea, and these spinose extensions, as resulting from an external generative epithelium from which byssal

Figs 112–119 *Tylothyris laminosa* (M'Coy) from Co. Fermanagh. Fig. 112a–e, complete specimen viewed dorsally, ventrally, anteriorly, laterally and posteriorly. BB63610, $\times 1.5$. Fig. 112f, same specimen showing stegidial plates. BB63610, $\times 3$. Fig. 113a–c, juvenile ventral valve viewed externally, posteriorly and internally; the juvenile dental plates are arrowed. BB63617, $\times 4$. Fig. 114, interior of adult dorsal valve showing the striated cardinal process (arrowed) and strong inner socket ridges. BB63611, $\times 1.5$. Fig. 115, interior of young incomplete ventral valve, showing dental plates and low median septum (arrowed). BB63616, $\times 4$. Fig. 116, interior of adult ventral valve, showing the lateral deflection of the ridges extending forward from the dental plates and slightly raised adductor muscle scars (arrowed). BB63613, $\times 1.5$. Fig. 117a, b, incomplete young dorsal valve viewed externally and internally. BB63615, $\times 4$. Fig. 118, internal view of incompletely silicified ventral valve, showing the adductor muscle scars medially, parts of the dental plates and parts of the pitted areas of the internal surface. BB63600, $\times 1.5$. Fig. 119a–c, dorsal, ventral and posterior views of juvenile shell; note the asymmetrical growth of the ears and on Fig. 119c the grooves near the edges of the delthyrium. BB63612, $\times 4$.



filaments grew, attaching the shell to the substrate. I find his argument for a byssal brush covering the interarea unconvincing, and he ignores the important geometrical constraints imposed on the shell growth by the straight, wide hinge line. The fine reticulate pattern of growth lines and perpendicular striations possibly results from unusually thickened periostracal material, developed at the valve margin, leaving growth traces across the interarea. Medially, this periostracal covering would have protected the delthyrial opening and dorsal ends of the diductor muscles. Elsewhere along the hinge line it would have sealed the posterior commissure and, perhaps, aided in the holding of the valves together. Sufficient elasticity would have been necessary to allow hinge movement, and the periostracum on the interareas may have assisted this movement.

The shell articulation is such that the valves would not have held together for long after death of the animal and decay of the articulatory muscles. Only four shells remain articulated and as two of these are young it may be that the population was killed, perhaps by the arrival of unusual quantities of fine sediment. Of the disarticulated valves many show signs of having been broken prior to silicification, and are infested by organisms such as tubiculous worms, fenestrate bryozoan holdfasts or the microscopic ramifications of ctenostomatous bryozoans (Brunton 1966b) or phoronids. These features indicate that some dead shells remained on or close to the substrate surface for an appreciable length of time before becoming deeply buried.

RANGE. The species is well known in Belgium, where fine silicified specimens have been collected from the late Tournaisian shales in the Tournai region. Some of these specimens match those from Fermanagh very closely in size and external features. One difference, however, is that the Belgian specimens tend to have more strongly developed, higher, fastigia (term of Cooper & Grant, 1976, for the median dorsal crest), creating well-differentiated folds of the anterior margins, while the dorsal fastigia of Fermanagh shells do not rise much above the bordering ribs. Unfortunately, material from Hook Head, the type locality, is crushed and detailed development of the fastigium and sulcus cannot be observed. Ventral valve interiors, available from Hook Head, Belgium and Fermanagh, show that the development of shell thickening in the ventral umbo, around the dental plates, ventral muscle scars and median septum, varies during late ontogenetic stages to such an extent that comparisons are of little value without the benefit of large collections. Specimens from all three localities seem to have become equally thickened late in their lives, but those from Hook Head and Fermanagh retained a prominent median septum which extends well beyond the dental plates and muscle scars, to nearly half the valve length (Figs 111, 116). However, it is seldom well preserved.

Carter (1967) described *T. brevaurita* from late Tournaisian rocks of central Texas, and compared the species to others from the Mississippian of North America. None of these closely resembles *T. laminosa* although *T. brevaurita* retains a distinct ventral median septum.

Two species of *Tylothyris* have been described from Australia which resemble *T. laminosa*. Firstly *T. planimedia* Cvancara (1958), originally described from New South Wales in rocks thought to be late Tournaisian in age, is now, according to Roberts (1975 and personal communication) considered as Viséan, equivalent to the British D₁, Asbian stage. Gaetani (1968) recognized this species in rocks of the central Elburz, Iran, which appear to be of a late Tournaisian age. The second species is *T. transversa* Roberts, 1971, from the Enga Sandstone (late K zone, Tournaisian) of north-west Australia. Roberts' species differs from *T. laminosa* in having a lower ventral interarea, resulting in the umbones remaining narrowly separated and in the delthyrial angle being 50°–55°, as compared to the 35°–40° in *T. laminosa* from Hook Head. The fold (fastigium of Cooper & Grant, 1976) and sulcus are narrower than in *T. laminosa*, while those of *T. planimedia* have flat bases, with the hint of a faint median rib. Details of the delthyrium, apical callosity and ventral median septum are commonly considered as providing distinctive features. However, in the silicified Fermanagh fauna these features are variable. The delthyrial angle increased with age, the apical callosity increased and the median septum became increasingly buried by the deposition of secondary shell in the ventral valve umbo. For these reasons I do not feel that the distinctions made between the two Australian species, using these features, are meaningful.

Geographically *Tylothyris* species similar to *T. laminosa* extend from western Europe, through the Middle East to Australia. North American *Tylothyris* species are less closely related to *T. laminosa*. Recently Jin & Fang (1983) used the species name for early Carboniferous specimens they described from Yunnan, China, but appear to have ignored its designation as type species of *Tylothyris* by assigning it to *Spinocyrtia* Frederiks, a genus typical of the Devonian.

Stratigraphically, *T. laminosa* is known from the late Tournaisian, in the type locality and in Belgium, and from mid-Viséan rocks in north-west Ireland, including the present Fermanagh fauna. This long range is unusual for brachiopod species, but some are known with equally long or longer ranges. Perhaps significantly, another Hook Head species, *Brochocarina wexfordensis* (Smyth), also occurs in Fermanagh as has been described (Brunton 1968).

When first describing *Tylothyris* North included *T. subconica* (Martin 1809), divided as two subspecies, *subconica* (Martin) and *castletonensis* North, 1920, from D Zone (Asbian and Brigantian) rocks of northern England and of Ireland. These are distinctive shells with high, almost flat, ventral interareas, giving an outline reminiscent of *Syringothyris* or *Pseudosyrinx*.

Family **PAECKELMANELLIDAE** Ivanova 1972

Subfamily **STROPHOPLEURINAE** Carter 1974

DIAGNOSIS (emended). Small to medium transverse Paeckelmanellidae with simple lateral costae ornamented by lirae and commonly with strongly developed growth lines. Fold and sulcus commonly non-costate, with or without median rib and groove; sulcus bounding ribs commonly accentuated, as are corresponding dorsal grooves. Ventral interarea large and denticulate. Dental plates short or heavily thickened. Dorsal sockets small and closely set, cardinal process commonly supported medially by short ridge; shell substance impunctate.

DISCUSSION. While preparing his 1974 paper, Carter was apparently unaware of Ivanova's (1972) classification of spiriferids. In this general study Ivanova erected the new family Paeckelmanellidae, within the superfamily Syringothyridacea. In 1981 Ivanova took the matter a stage further in elevating her 1972 new family to superfamily level – the Paeckelmanellacea. Her familial taxonomy (Ivanova 1981) retained the family Paeckelmanellidae, within which she placed three subfamilies, the Strophopleurinae Carter, the Pterospiriferinae Waterhouse, and the Paeckelmanellinae Ivanova. Within Carter's (1974) subfamily she placed *Strophopleura* Stainbrook, *Acuminothyris* Roberts, *Fusella* M'Coy and *Voiseyella* Roberts. Carter (1974) did not include *Fusella* in his classification, but several of the genera he did include within the Strophopleurinae have been assigned by Ivanova (1981) to her Paeckelmanellinae or to Waterhouse's Pterospiriferinae. While I find it unfortunate that a family, or superfamily, should have been based on an imperfectly known genus like *Paeckelmanella* Likharev, I agree with Ivanova's concept of a family for the genera she has included in the Paeckelmanellidae.

Brunton & Rissoné (1976) utilized the subfamily Strophopleurinae in their redescription of the genus *Fusella* M'Coy, but erred in assigning it to the family Mucrospiriferidae. The familial diagnostic importance of a denticulate hinge line was stressed by Carter (1974) and Ivanova (1981), and is helpful in distinguishing between members of this family and the Mucrospiriferidae.

Genus **FUSELLA** M'Coy 1844

TYPE SPECIES. *Spirifer fusiformis* Phillips, 1836: 210; pl. 9, figs 10, 11, by original designation of M'Coy (1844: 132).

DIAGNOSIS. Small (commonly less than 30 mm wide) to medium-sized, but strongly transverse, fusiform shells, with subcircular lateral profile. Ventral interarea wide, concave and denticulate. Costate ribbing, ill-defined on fold and sulcus, but prominent bordering sulcus. Dental plates close, subparallel and within sulcus.

DISCUSSION. The genus formed the subject of papers by Brunton & Rissone (1976) and Waterhouse (1970). Because the single specimen of *F. fusiformis* described by Phillips is poorly preserved and the species is rare, there being only one other specimen known to me (Davidson Collection specimen B7379 from Dovedale, Derbyshire), both species and genus have remained ill-defined and the genus name has been used incorrectly, especially in some Russian literature. Both specimens of *F. fusiformis* were described and figured by Brunton & Rissoné (1976), who, following Brunton & Champion 1974, suggested that *Spirifer rhomboidea* Phillips belonged to the genus and described its internal structures, as a guide to those of *Fusella*. *Fusella rhomboidea* is a rare member of the Fermanagh silicified faunas.

Fusella rhomboidea (Phillips)

Figs 120–127

- v* 1836 *Spirifera rhomboidea* Phillips: 217; pl. 9, figs 8, 9.
 1858 *Spirifera convoluta* var. *rhomboidea* Phillips; Davidson: 35; pl. 5, figs 2–8.
 v 1974 *Fusella rhomboidea* (Phillips) Brunton & Champion: pl. 111, figs 6, 7.
 1976 *Fusella rhomboidea* (Phillips); Brunton & Rissoné: pl. 1, figs 13–17.

DIAGNOSIS. Relatively large *Fusella* about twice as wide as long, with prominent fold, sulcus and costae. Single low dorsomedian costa; first pair of ribs bordering fold bifurcate close to umbo. Ventral interarea denticulate, high and strongly concave. Teeth supported by dental ridges and plates diverging slightly anteriorly and onto valve floor, on flanks of ventral sulcus.

LECTOTYPE. *Spirifer rhomboidea* Phillips, figured 1836: pl. 9, fig. 8; from Bolland, Yorkshire. Gilbertson Collection, BM(NH), B236. Lectotype selected by Brunton & Rissoné, 1976 (Fig. 120).

DESCRIPTION. Fusiform shells throughout ontogeny with a length about half the total width and a little greater than the thickness. On each side there are up to twelve ribs which diminish in size laterally. A low median costa may be developed on the dorsal fold, and the first pair of costae bordering the fold bifurcate within 2 mm of the umbo. Similarly, the pair of costae bordering the

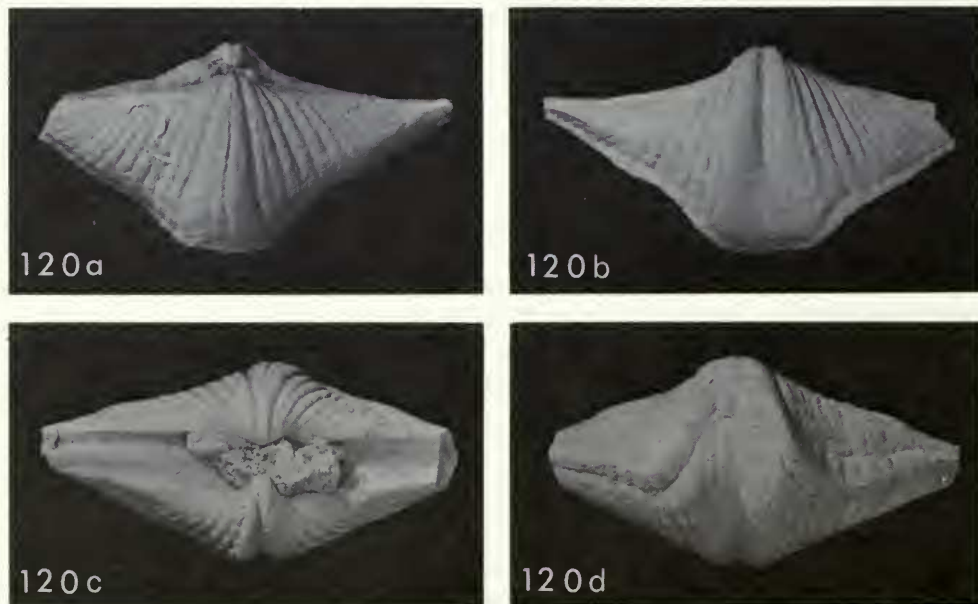


Fig. 120 *Fusella rhomboidea* (Phillips). The lectotype, selected Brunton & Rissoné (1976), from the Viséan of Bolland, Yorkshire, viewed (a) dorsally, (b) ventrally, (c) posteriorly and (d) anteriorly; the shell is stripped from the ventral interarea so the denticulation does not show. B236, $\times 2$.

ventral sulcus may bifurcate laterally, close to the umbo, and a little later in ontogeny a median branching may occur so as to give a pair of weak costellae within the sulcus.

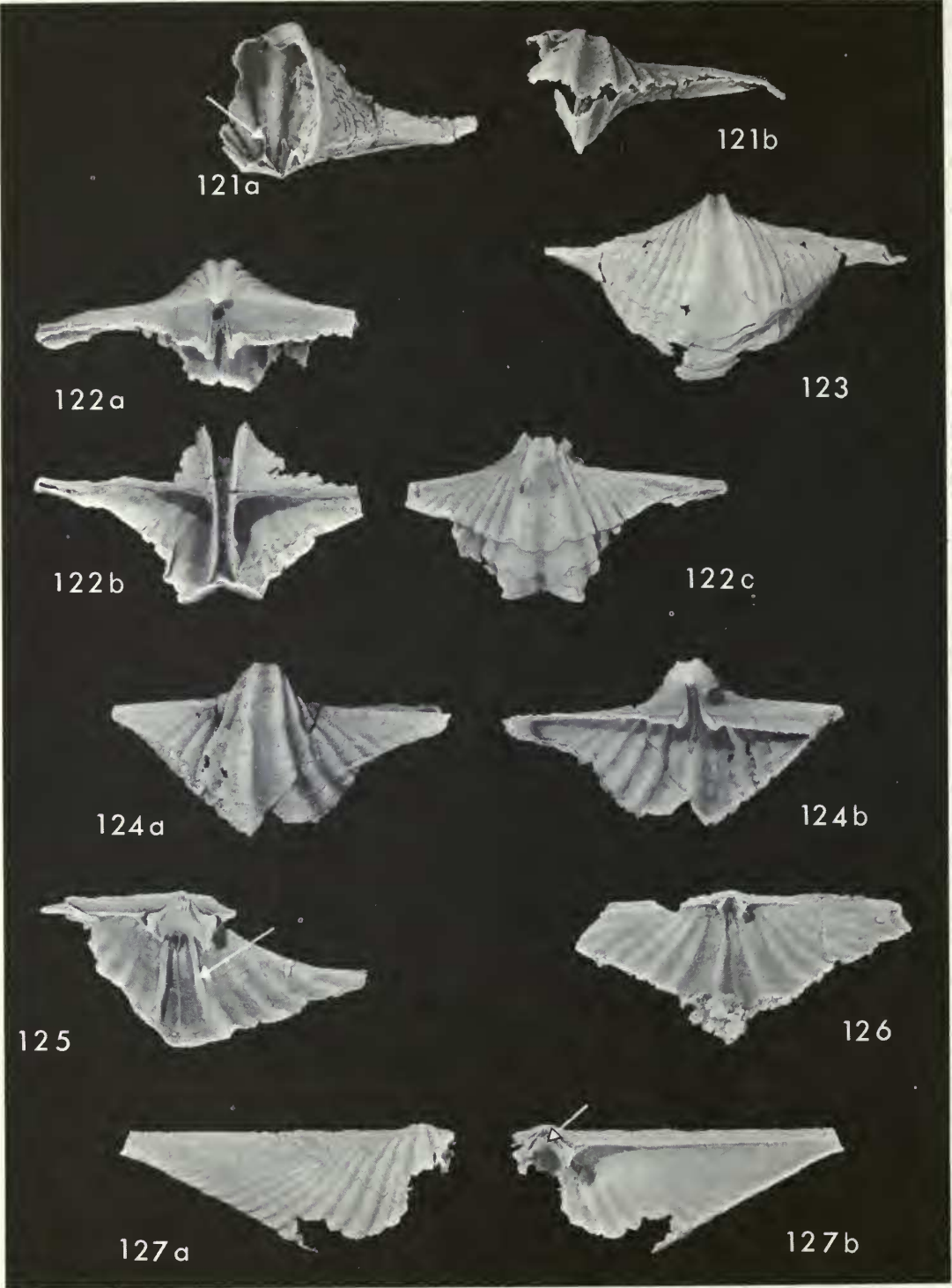
External micro-ornamentation consists of a fine radial lineation (observed only on the silicified specimens), of about fifteen ridges per mm width medially on the ventral valve at about 5 mm from the umbo.

The ventral interarea is high, with a curvature of about 180° , and extends the complete width of the hinge line (Fig. 122a, b); it is irregularly denticulate. The dorsal interarea is short (only about 0.2 mm) and may not extend for the full hinge width.

ONTOGENY. Within the ventral valve of young shells the delthyrium is open but in older valves apical secondary thickening, between the dental plates, partially fills the cavity almost to the level of the interarea (Fig. 122a). This infilling between the dental plates may extend anteriorly in the delthyrium for up to 2 mm. The delthyrium is narrow, its margins diverge at $20\text{--}30^\circ$ and are differentiated from the interarea by shallow grooves and ridges (Fig. 124b), which both represent the traces of the teeth and show that a delthyrial cover was probably present in life. The teeth are triangular in outline and cross section; they do not extend far beyond the hinge line. In early growth stages the teeth were supported by subparallel dental plates about 0.2 mm apart. As the interarea grew anterodorsally, and away from the floor of the valve, the dental plates grew anteriorly only far enough to support the teeth perpendicularly to the valve floor. Thus adult teeth are supported by dental ridges which merge posteroventrally into the dental plates (Fig. 122b). These converge slightly below the interarea and then diverge onto the valve floor within 1 mm on either side of the mid-line. They do not continue anteriorly on the valve floor as ridges, nor is there a median ridge, other than the internal expression of the median sulcus. The muscle scars are indistinct, but the adductor scars were confined posterolaterally, between the dental plates, and extended anteriorly for over half the valve length with a narrowly triangular outline. The diductor scars appear to have flanked the adductor scars and to have remained within the confines of the ventral sulcus. (It may be that the anterior portion of the scars described above as adductors were the anteromedially joined diductor scars. If so the adductor scars extended only a short distance in front of the dental plates and were surrounded anterolaterally by the diductor scars.)

Within the dorsal valve the sockets are shallow, being floored by fulcral plates extending from below the hinge line to the bases of the inner socket ridges (Fig. 125), which diverge at about 75° from each other. A pair of plates diverge dorsally from the inner socket ridges either side of the small longitudinally striate cardinal process. These plates (crural bases) converge slightly towards the valve floor, to which they are fused only posteriorly (Fig. 127b). In larger specimens (about 14 mm wide) the inner socket ridges and crural bases converge to the valve floor more strongly and secondary shell developed apically (Fig. 125). The crura extend subparallel to one another from the anterodorsal extremities of the socket/crural plates, but the form of the spiralia is unknown. A pair of ridges developed during ontogeny which extend anteriorly from the crural bases along the internal edges of the dorsal fold for three-eighths of the valve length (Fig. 125); they enclose the narrowly ovate adductor muscle scars which, in adult valves, were separated medially by a low ridge. With the exception of the ventral umbo and between the dental plates, the shell substance of the valves remained thin; it is impunctate and probably did not include the development of an internal tertiary layer.

DISCUSSION. This species is not common in the Fermanagh faunas, being represented by fifteen incomplete ventral valves, three dorsal valves and two incomplete young shells from the Sillees river locality. This, however, is sufficient to allow a full description of internal morphology for the first time. In addition a specimen of *F. rhomboidea* (B7387) from the Cork area of Ireland was sectioned at narrow intervals and shows internal structures identical with the silicified material. The differentiation and development of new structures during growth is difficult to distinguish owing to the shortage of material. In the ventral valve secondary shell infills the space between the dental plates apically and in two adult valves the bases of the dental plates suddenly widen anteriorly, probably representing the anterolateral growth of the plates around the posterior margins of the adductor muscles. In the older dorsal valves the crural bases fused to



posteriorly prominent ridges bordering the adductor muscle field, and a median ridge, or myophragm, developed between the adductor muscle scars.

Four specimens of *F. rhomboidea* exist in the Gilbertson Collection of the BM(NH), including the lectotype. These are described as coming from Bolland and are probably of low to mid Viséan age. Additional conspecific specimens in the BM(NH) came from low Viséan rocks of north Staffordshire and there is material from the Cork area of Ireland. A single large specimen (B48081) with broken tips to its cardinal extremities (50 mm wide), from the high Viséan of Narrowdale Hill, Staffordshire and labelled *F. grandicostata* (M'Coy), has external characteristics very similar to those of *F. rhomboidea*. Growth lines on this specimen show that at a width of 32 mm the dorsal valve was about 14 mm long and was ornamented by nine pairs of ribs, of which the median pair branched close to the umbo. For a given valve size the ribs are wider on this specimen than on *F. rhomboidea*, and growth lines, developed early in ontogeny, show that a wide fusiform shape did not develop until the shell was at least 15 mm wide. This, the overall size and coarser ribbing distinguishes M'Coy's species *grandicostata* from *rhomboidea*. The internal morphology of M'Coy's species is unknown so it is impossible to be sure of its generic position. However, many of its external characteristics are like those of *Spirifer strangwaysi* de Verneuil, the type species of *Brachythyridina* Frederiks 1929, and if *grandicostata* M'Coy proves to be devoid of dental plates then it should be assigned to that genus.

Other species with which *F. rhomboidea* can be compared are the young of *Spirifer triangularis* J. de C. Sowerby, placed by Muir-Wood (1951) into *Fusella*, but which differ in having a high carinate fold and prominent ventral median rib in the sulcus. Davidson (1858) placed *rhomboidea* into synonymy with *S. convoluta* Phillips, but the latter is distinct in reaching a far greater size and in being more than four times as wide as long. However, growth lines show that when at the size of *F. rhomboidea* the anterior fold of *S. convoluta* was less well developed. The interior of *S. convoluta* is poorly known, but its close dental plates and denticulate hinge line are suggestive of assignment to *Fusella*.

The *Voiseyella* species *anterosa* Campbell, *novamexicana* Miller, *texana* Carter and *mundula* Rowley from Lower Carboniferous strata of Australia and North America all differ in having a more strongly developed imbricate external ornamentation than *F. rhomboidea*. Furthermore, it seems clear that none of the costae branch in these species and their width is commonly about 20 mm (i.e. less than that of mature *F. rhomboidea*). In addition to the above species there are two very similar species, *Spirifer biplicatus* Hall and *S. biplicoides* Weller, from the Kinderhook strata of Iowa, U.S.A. Judged from the external features described by Weller (1914) these species might equally well belong within either *Fusella* or *Voiseyella*. The ventral valve of *S. biplicoides* illustrated by Weller (1914: pl. 39, fig. 29) is very similar to *F. rhomboidea* and dorsal valves have a shallow median groove on the fold, as do the type species of both these genera. There are clear similarities between species of *Fusella* and *Voiseyella* but externally the two groups can be distinguished by the lack of strong, imbricate growth lines on *Fusella* species.

Paucity of material and information on internal morphology of some species inhibits the working out of a phylogeny for *Fusella*. It is possible, however, that a species in the small upper Devonian genus *Strophopleura* gave rise to the Tournaisian species of *Voiseyella* and thence to

Figs 121–127 *Fusella rhomboidea* (Phillips) from Co. Fermanagh. Fig. 121a, b, incomplete juvenile shell viewed dorsally and anteriorly; in Fig. 121a the crura (arrowed) are shown. BB61617, $\times 6$. Fig. 122a–c, incomplete adult ventral valve viewed posteriorly, internally and externally; in Fig. 122a the thickened shell in the apex of the delthyrium has been bored. Note the close, subparallel dental plates. BB61612, $\times 3$. Fig. 123, exterior of a large ventral valve; note the fusiform ears. BB61614, $\times 2$. Fig. 124a, b, exterior and posterodorsal views of a young ventral valve showing asymmetrical growth and, in Fig. 124b, shallow grooving near the delthyrial margin and a bore-hole at the side of the umbo. BB61613, $\times 5$. Fig. 125, internal view of part of an adult dorsal valve showing the cardinalia ridges (arrowed) formed only late in growth. BB61611, $\times 4$. Fig. 126, interior of young dorsal valve with only lightly developed cardinalia. BB61616, $\times 5$. Fig. 127a, b, external and internal views of incomplete dorsal valve showing the diminution of ribs laterally, dorsal interarea and striate cardinal process (arrowed). BB61615, $\times 3$.

the principally Viséan *Fusella*. The Carboniferous to Lower Permian genus *Brachythyris* may have evolved from this group, as may also the northern species of the Permian genera *Paeckelmanella* and *Pterospirifer*. If so there was an evolutionary trend towards an increase in overall size and, in the Permian, a stronger development of dental plates in these younger genera.

Family **BRACHYTHYRIDIDAE** Frederiks 1919

The family was redefined by Carter (1974) to include only those genera lacking dental plates (adminicula). He included *Brachythyris* M'Coy, *Ella* Frederiks, *Pustuloplica* Waterhouse, *Litothyris* Roberts, *Meristorygma* Carter and *Skelidorygma* Carter. Until Carter defined *Skelidorygma*, *Brachythyris* had contained species lacking ribs on the dorsal fold (fastigium) and ventral sulcus, as well as those having entirely ribbed shells. Carter placed in *Skelidorygma* those species with entire ribbing, but lacking denticulate hinge lines.

Genus **BRACHYTHYRIS** M'Coy 1844

TYPE SPECIES. *Spirifera ovalis* Phillips 1836: 219; pl. 10, fig. 5, from the Viséan of Bolland, Yorkshire. **Lectotype**, here selected, figured by Phillips from the Gilbertson Collection in the BM(NH), B247.

DIAGNOSIS. Hinge markedly narrower than shell width or with wider but very short ventral interarea laterally, commonly denticulate. Simple broad ribs, absent or only weakly developed in sulcus or on fastigium. No dental plates.

DISCUSSION. The type species of *Brachythyris* was not specified by M'Coy (1844) but was designated in 1908 by Buckman who pointed out that the type species, as figured by M'Coy, might be recognized as *Spirifera ovalis*. The illustration to which Buckman referred is figure 20, p. 128 of M'Coy's *Synopsis* (1844) and although this figure is not named, other than by reference to *Brachythyris*, it clearly depicts *B. ovalis*. In George's redescription of the genus in 1927 he quoted *B. ovalis* (Phillips) as type species, and Pitrat, in the *Treatise* (Williams *et al.* 1965), gave the designation as being by M'Coy, and thus accepted the unnamed fig. 20 (1844) as being sufficient indication of the intended type species. Carter (1967) provides a full reference list of the use of the name *Brachythyris*.

Brachythyris ovalis, *S. integricostus* Phillips and *S. pinguis* J. Sowerby are all somewhat similar species and the morphological differences between them were fully discussed by Davidson (1859). He pointed out that the length to width ratio of these shells is variable, so that although *B. ovalis* is typically longer than wide, in some individuals the reverse is true. This type of variation can be matched in assemblages of Recent brachiopods (McCammon & Bucksbaum 1968). The style of ribbing is characteristic of the genus; well-developed broad, rather flat ribs which do not branch except those that border the ventral sulcus or, less commonly, the dorsal fold, whilst still close to the umbones. In *B. ovalis* the dorsal fold (fastigium) is smooth, whilst weakly-developed costellae may border the sulcus. In *Brachythyris pinguis* the fastigium lacks ribs but has a median groove and the sulcus may be weakly ribbed, especially marginally. The complete ribbing of *S. integricostus* could be considered as one extreme of the variation displayed in this feature by contemporaneous species. Nevertheless, the adult shapes of these three species are distinctive, *B. ovalis* being longer than wide, *S. integricostus* wider than long and *B. pinguis* somewhat quadrate in outline, deep-bodied and more deeply sulcate than the others. The Phillips species *S. duplicicosta* has distinctive finer, branched ribbing, unlike that of *Brachythyris* species. In addition, although its ventral interarea is narrow compared to the width of the shell, it has strong dental plates and so cannot be a *Brachythyris*. Another species having affinities with *Brachythyris* is *S. rotundata* J. Sowerby. Its ribbing is like that of the much smaller *B. ovalis*, but even the juvenile outline of *S. rotundata* seems to have been broader than long, and the adult hinge line is wide, unlike that of *Brachythyris* species as usually defined. A difficulty lies here in the fact that young specimens, up to about 50 mm wide, may have distinctly narrow hinge lines (under 30 mm) and so fall well

within the definition of *Brachythyris*. As the general characteristics of this species, including its lack of dental plates, indicate to me an assignment to *Brachythyris* I have extended the genus diagnosis to include specimens with wider hinge lines, but only if accompanied by very short ventral interareas, so that the umbones remain close to each other throughout ontogeny. *Spirifer integricostus* Phillips has normally been considered as a *Brachythyris* species, but its entire ribbing fits it better into Carter's *Skelidorygma*. A problem with this assignment is that *S. integricostus* has a weakly denticulate hinge line, while species in Carter's genus should not. As denticulation is not always easy to distinguish I widen the diagnosis of *Skelidorygma* to include *S. integricosta*, a species found rarely in the Fermanagh silicified faunas.

Genus *SKELIDORYGMA* Carter 1974

TYPE SPECIES. *Spirifer subcardiiformis* Hall 1858, from the Salem Limestone (Viséan) of mid-continental North America, by original designation of Carter (1974: 692).

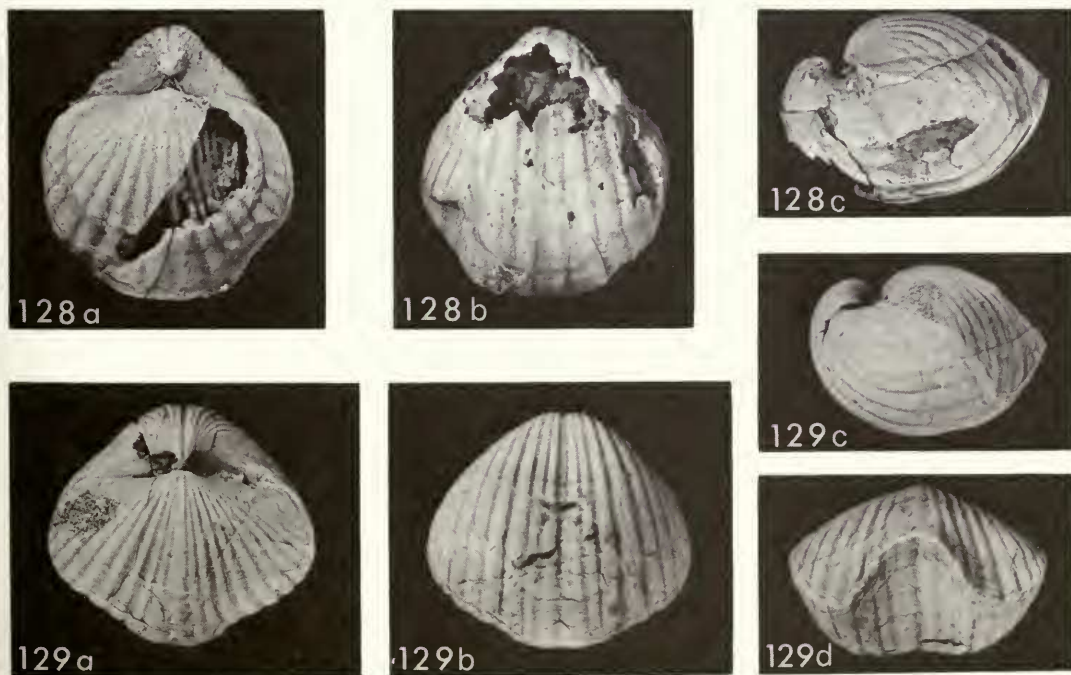
DIAGNOSIS. Ovate to subcircular Brachythyrididae, entirely ribbed with simple flattened costae, but branching medially on gentle fold and sulcus. Ventral interarea weakly to not denticulate.

Skelidorygma integricosta (Phillips)

Figs 128, 129

- v* 1836 *Spirifera integricosta* Phillips: 219; pl. 10, fig. 2.
 1844 *Brachythyris integricosta* (Phillips) M'Coy: 145.
 1859 *Spirifera integricosta* Phillips; Davidson: 55; pl. 9, figs 13–19.

LECTOTYPE. Here selected from the Gilbertson Collection, BM(NH), B269, being the specimen figured by Phillips and refigured here (Fig. 129). It is from the Viséan of Bolland, Yorkshire.



Figs 128–129 *Skelidorygma integricosta* (Phillips). Fig. 128a–c, incomplete young shell from Co. Fermanagh; viewed dorsally (showing part of the spirallium), ventrally and laterally. BB63694, $\times 2$. Fig. 129a–d, lectotype, here chosen, from the Viséan of Bolland, Yorkshire; viewed dorsally, ventrally, laterally and anteriorly. B269, $\times 1$.

DIAGNOSIS. Broadly to very broadly ovate in outline, strongly biconvex shells. Ventral umbo incurved, close to dorsal umbo, giving concave, weakly denticulate ventral interarea about two-thirds as wide as shell. Ribbing entire, mostly with simple, low, rounded costae widening anteriorly. Micro-ornamentation of non-lamellose growth lines. Small deltidial plates, dental plates lacking. Shell impunctate.

DISCUSSION. Only one almost complete young shell, believed to be of this species, has been collected from the silicified limestone. It is 18.5 mm long, 16.8 mm wide and 12.7 mm thick; it is thus rather more like *Brachythyris ovalis* in outline than the lectotype of *S. integricosta*. However, the entire ribbing and strong biconvexity of the Fermanagh shell are characteristic features of this species rather than of *B. ovalis*.

Although the silicified specimen is broken, so as to allow a view of the brachidium with about nine coils on each side, siliceous deposits in the umbones obscure all details of the cardinalia, making it impossible to add to the descriptions previously given for this species.

The lectotype of *S. integricosta* is about the same size as the holotype of the genotype *Skelidorygma subcardiiformis* (Hall) (Carter 1974: pl. 4, figs 8–12) and both have similar shapes, other than in the dorsoventral outline where the American species is relatively longer. It differs also in having slightly coarser ribs, a non-denticulate hinge line and weaker uniplicate anterior commissure.

Superfamily **SPIRIFERINACEA** Davidson 1884

Family **SPIRIFERINIDAE** Davidson 1884

Genus **SPIRIFERELLINA** Frederiks 1919 (1924)

TYPE SPECIES. *Terebratulites cristatus* von Schlotheim, 1816, from the Zechstein of Glücksbrunnen, Thüringen. Lectotype selected by Campbell (1959) from the Schlotheim Collection of the Geologisch-Paläontologisches Institut und Museum, Berlin.

DIAGNOSIS. Very broadly obovate in outline, strongly ventribiconvex in profile. Commonly eight (dorsal valve nine) strong angular plications, with medium sulcus not strongly differentiated. Ventral interarea not extending to maximum shell width. Ornamentation of distinct growth lines and micro-ornamentation of pustules and microspines. Ventral median septum is high posteriorly and extends anteriorly beyond the dental plates, with posteriorly concave anterior edges. Inner socket ridges are supported by plates to the valve floor.

DISCUSSION. Campbell (1959), recognizing the common confusion between *Spiriferellina* and *Punctospirifer* North, redescribed the type species of these genera. He had, however, to rely upon serial sections of specimens for the internal morphology and was unable to be precise about the relationships of the dental plates and median septum in *Spiriferellina cristata*, the type species. The silicified Viséan species *S. insculpta* (Phillips), described below, is very similar to *S. cristata* externally and can be considered to be congeneric.

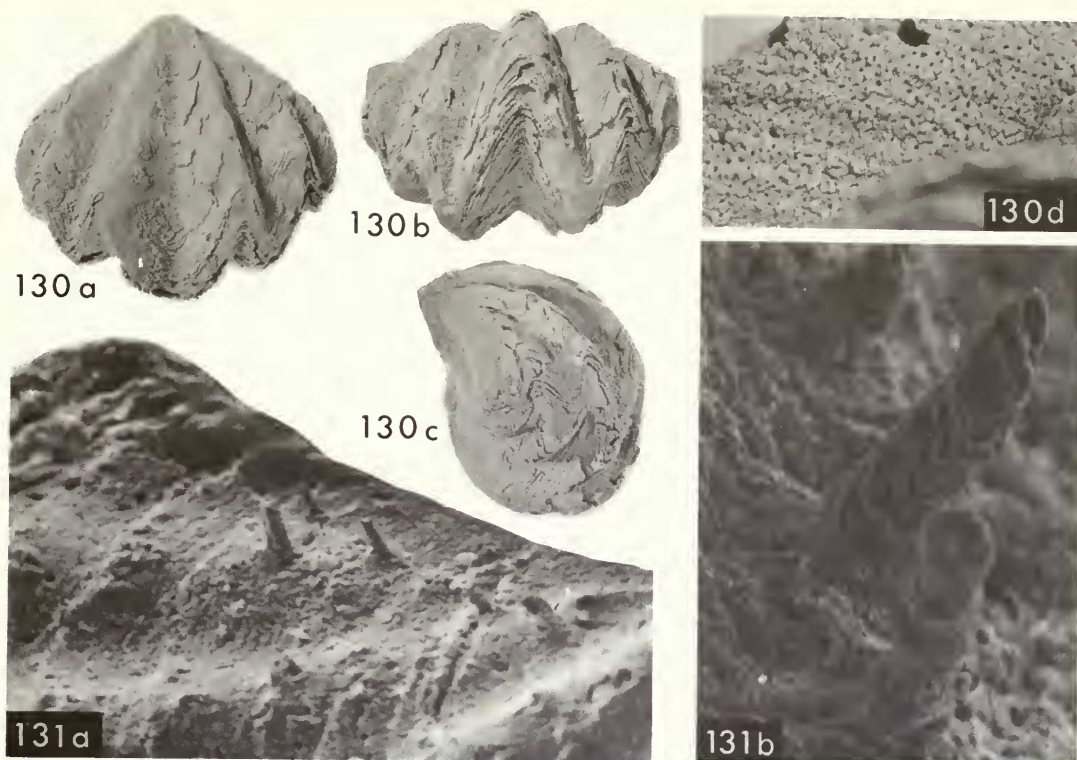
Spiriferellina insculpta (Phillips)

Figs 130–143

- v* 1836 *Spirifera insculpta* Phillips: 216; pl. 9, figs 2, 3.
- 1858 *Spiriferina* (?) *insculpta* (Phillips) Davidson: 42; pl. 7, figs 48–55.
- v. 1863 *Spiriferina insculpta* (Phillips); Davidson: pl. 52, fig. 14 (not fig. 15).
- 1920 *Spiriferina insculpta* (Phillips); North: 217; pl. 13, fig. 11.

LECTOTYPE. Here selected, *S. insculpta* Phillips from the Gilbertson Collection, BM(NH), B304. The specimen comes from the Carboniferous Limestone of Bolland, Yorkshire and was that figured by Phillips in 1836 (Fig. 130).

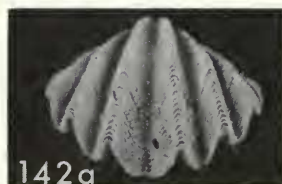
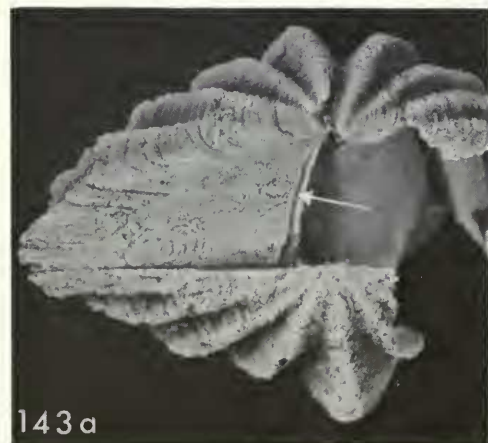
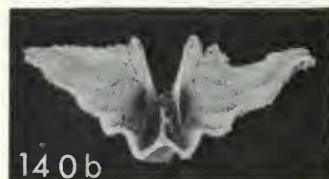
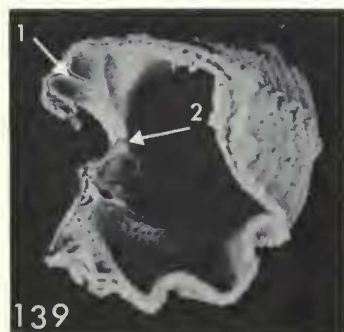
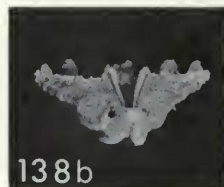
DIAGNOSIS. Transversely broadly elliptical in outline, ventribiconvex in profile with high, only slightly curved ventral interarea. Strong angular costae, normally five or seven on dorsal valve. Weakly lamellose and minutely spinose external ornamentation. Sockets and crural bases elevated above valve floor.



Figs 130–131 *Spiriferellina insculpta* (Phillips). Fig. 130a–d, lectotype, here chosen, from the Viséan of Bolland, Yorkshire; viewed ventrally, anteriorly and laterally (with the ventral valve uppermost), $\times 2$, and an enlarged area of the shell showing the endopunctuation, $\times 10$. B304. Fig. 131a, b, from Co. Fermanagh, showing details of the microspinous external ornamentation. BB61626, S.E.M. (a) $\times 50$, (b) $\times 200$.

DISCUSSION. For its time Phillips' (1836) original description is quite good—'Cardinal area large; the mesial and two or three lateral folds very bold, acute, and strongly striated across.' North (1920) gave a full description of the exteriors but was incorrect in suggesting that Davidson (1858) had refigured the type specimen and that the dorsal valve has one more rib (costa) than the ventral valve; in fact the reverse is true. Dorsal valves always have an odd number of costae, one less than ventral valves, a fact that is dictated by the morphology of the commissure (Fig. 130b).

S. insculpta is more rounded in outline than the other *Spiriferellina* species from our Lower Carboniferous rocks and the dorsal valve has a greater convexity than has the closely related species *S. perplicata* (North). Because of this greater curvature the internal morphology also differs. In the flatter valve of *S. perplicata* the sockets and crural bases are close to, and fuse with, the inside surface of the valve; in *S. insculpta* the valve curvature keeps the sockets and crural bases separate from the valve floor (Fig. 132b). On the largest silicified valves traces of muscle scars can be seen on the crural bases (= inner socket plates), which probably represent the sites of attachment of the pedicle adjustor muscles. The dorsal adductor muscle scars are just anterior of the crural bases, within the trough of the dorsal fold and, in adult specimens, are separated medially by a low ridge (Fig. 133). Unfortunately, in no specimen are the spiralia preserved beyond the first dorsomedian primary lamellae; although at a distance of about 2.0 mm from the dorsal umbo there are two ventrally projecting prongs, no jugum has been observed. Campbell (1959) was unable to describe the interior of *S. cristata*, the type species, from the evidence of serial sections; he believed there to be no jugum in *Punctospirifer*, but he recorded one in the



North American Mississippian genus *Reticulariina*. The evidence afforded by this silicified material is equivocal and it is impossible to say if, in life, a complete jugal saddle connected the two prongs which are preserved in some specimens. At any event the mouth section of the lophophore would have been in this region, close to the body wall.

The ventral valve interior of *S. perplicata*, as seen in silicified specimens described by Brunton & Champion (1974) from Staffordshire, differs only slightly from the Fermanagh specimens of *S. insculpta*. The dental plates are short in both species but those of *S. insculpta* are even less well developed; they recede strongly below the ventral interarea and leave the teeth and distal (dorsal) half of the delthyrial edges unsupported, save for slight dental ridges (Figs 138a, 140b). The anterior edges of the dental plates diverge slightly to the valve floor where they join onto the lateral slopes of the median pair of costae (Fig. 136). In *S. perplicata* the dental plates fuse to the valve floor along the crests of the median pair of costae. The median septum is high posteriorly and sharply truncated anteriorly, approximately at the same position behind the anterior margin of the valve as are the jugal prongs. It seems likely, therefore, that the anterior edge of the ventral median septum also marks the position of the body wall in the living animal. Ventral muscle scars have not been distinguished, but it is probable that the median septum was involved with muscle attachment.

ONTOGENY. The Fermanagh specimens range in width from 1.5 mm to nearly 10.0 mm. In the smallest shells there are only two ventral costae and no dental plates, but the median septum can be distinguished. By a width of 2.0 mm to 2.5 mm minute apical dental plates had started to develop and by a width of 4.0 mm these were clearly differentiated. By this time the full eight ventral costae can normally be distinguished (Fig. 138), and these valves change little during further stages of growth. In a dorsal valve 4 mm wide the cardinal process is difficult or impossible to see, the crural bases remain joined to the valve floor anteriorly and there is no sign of the median ridge. The development of the cardinal process varies considerably, but commonly by a valve width of about 6 mm it can be recognized as an apical, longitudinally striated, low knob. Normally a low median ridge developed anteriorly and the straited myophore region became increasingly posteriorly-directed during the later stages of ontogeny, a period in which the median and posterolateral adductor scar bounding ridges were developed (Figs 132, 135).

The development of the external lamellose ornamentation persisted throughout ontogeny, but posteriorly it was more delicate and abrasion normally made the umbones relatively smooth. Anteriorly the lamellae are prominent, 7 or 8 occurring in each 1 mm on the dorsal median rib. The edges of the lamellae are finely scalloped and rarely microspines are preserved (Fig. 131).

Figs 132–143 *Spiriferellina insculpta* (Phillips) from Co. Fermanagh. Fig. 132a–c, adult dorsal valve viewed internally, posterodorsally and externally. BB63553, $\times 3$. Fig. 133, internal view of shell with most of the ventral valve missing; the cardinalia and one crus (arrowed) can be seen. BB63562, $\times 5$. Fig. 134, immature dorsal valve interior showing the small juvenile crural bases, and endopunctuation. BB63556, $\times 5$. Fig. 135, immature dorsal valve interior with the median muscle scars just showing. BB63555, $\times 4$. Fig. 136a, b, incomplete ventral valve viewed internally and posteriorly to show the dispositions of the dental plates and median septum. BB63560, $\times 4$. Fig. 137a, b, young dorsal valve interior, prior to the growth of the cardinal process (cf. Fig. 132a), $\times 6$, and exterior, $\times 4$. BB63554. Fig. 138a, b, juvenile ventral valve viewed ventrolaterally and posteriorly, showing the young median septum (arrowed). BB63561, $\times 6$. Fig. 139, lateral view of an incomplete shell showing the ventral median septum (arrow 1), and a dental plate and its articulation with the inner socket ridge (arrow 2). BB63558, $\times 8$. Fig. 140a, b, incomplete ventral valve viewed posteriorly, with the umbo missing, to show a sectional-like view of the dental plates and median septum, and seen internally. BB63559, $\times 4$. Fig. 141a–c, juvenile shell viewed dorsally, ventrally and posteriorly, showing the lamellose external ornamentation. BB63557, $\times 4$. Fig. 142a, b, complete shell viewed anteroventrally and anteriorly (dorsal valve uppermost); there is a small bore-hole on the ventral valve anteromedially. BB63531, $\times 2.5$. Fig. 143a–c, incomplete adult shell viewed posteriorly, $\times 4$, showing ornamentation of the ventral interarea and groove near the delthyrial margin (arrowed), and ventrally and laterally, $\times 2$. BB63530.

Microspines have only been recorded previously on *Spiriferellina* species by Brunton (1976), although Campbell (1959) described 'nodes' on the exterior of the type species, *S. cristata*, which he said were not the 'bases of spinules'. I agree with Campbell's conclusion but it is now clear that in *S. insculpta*, at least, there was also a microspinous ornamentation during life. The majority of the microspines are not preserved and those that remain are usually between the costae anteriorly or on the posterolateral flanks of ventral valves where the largest seen is 0.5 mm long; only very occasionally have they been seen on dorsal valves and then close to the valve margin. It appears that during early stages of growth, up to a valve width of about 3 mm, the microspines developed principally along the crests of costae (Fig. 131a); scars from where they have broken leave a distinctive pattern. Later in life the microspines developed more regularly along each lamella, with a frequency of about ten per mm, so as to form continuous rows on and between the costae (Fig. 142). Being silicified it is impossible to describe the detailed structure of these spines, but the silica replicas indicate that they were hollow.

MICROSPINES. MacKinnon (1974) has described the spinose ornamentations of the endopunctate Liassic species *Spiriferina walcotti* (Sowerby). He showed that the spines became more densely distributed towards the valve margins, in a similar fashion to those of *S. insculpta*. He also discussed the means of growth of spines of *Spiriferina walcotti* and on *Spinatrypa* specimens. It seems likely that the main distinction between spiriferide and strophomenide tubular spines is that those of the Spiriferida developed by the folding under anteriorly of shell around short-lived marginal epithelial protuberances (Brunton 1976: text-fig. 1), as distinct from the prolonged wholly tubular development in the Strophomenida. When the mantle regressed, prior to the growth of the next lamina, spine growth probably ceased and continued shell deposition covered their internal openings. In particularly well preserved specimens a short indistinct line, immediately anterior of the spine base, marks the position in which the growing mantle margins re-fused.

The purpose of the microspinous ornamentation is not clear; it could have helped anchor the animals into a soft sediment or have been a protective adaptation against small crawling or encrusting predators. As the microspines must have grown at the valve margins, and these regions were probably always clear of the sediment substrate, the former suggestion is less likely than the latter. Most encrusting or boring organisms are likely to have found difficulty in 'sitting' on the external surface of *S. insculpta*; in about 200 valves only ten are bored, seven of which are ventral valves.

DISTRIBUTION. The species is much more common at the Sillees river locality than at the Carrick Lough locality, although the biggest specimen comes from the latter. In the collections of the BM(NH), specimens of *S. insculpta*, almost identical with the type specimen from Bolland, come from the D Zone 'reefal' limestones of Narrowdale, north Staffordshire. The species is also known from rocks of a similar age in Derbyshire, Anglesey and north-west Ireland. North (1920) indicated that the species, as well as his species *S. perplicata*, was to be found virtually throughout the D Zone. North's (1920) 'mut. K' of *S. perplicata* came from Tournaisian rocks of the south-west province. The extra pair of ribs commonly seen on the Fermanagh specimens of *S. insculpta* (as compared to the lectotype) may indicate a derivation from a pre-existing *S. perplicata*-like stock such as North's 'mut. K'. De Koninck (1887) has recorded the species from high Viséan strata at Visé, Belgium, and Sarycheva & Sokolskaja (1952) list it from near the Viséan/Namurian boundary of the Moscow Basin, but these are somewhat doubtful identifications and otherwise the species appears to be unknown outside the British Isles.

Other *Spiriferellina* species described from Viséan rocks elsewhere are uncommon. From the Utting Calcarene of north-western Australia (of a similar age to the Fermanagh fauna) Roberts (1971) described *Punctospirifer pauciplicatus*, but the illustrations are quite similar to *S. insculpta* and I think it should be assigned to *Spiriferellina*. Weller (1914) described *Spiriferina salemensis* from the Salem Limestone of Indiana (probably equivalent to early Viséan in age), and this species should probably also be assigned to *Spiriferellina*. Species attributable to the genus do not seem to have been described from Russian faunas of early to mid-Viséan age.

Superfamily **RETICULARIACEA** Waagen 1883Family **MARTINIIDAE** Waagen 1883Genus **MEROSPIRIFER** Reed 1948 (1949)

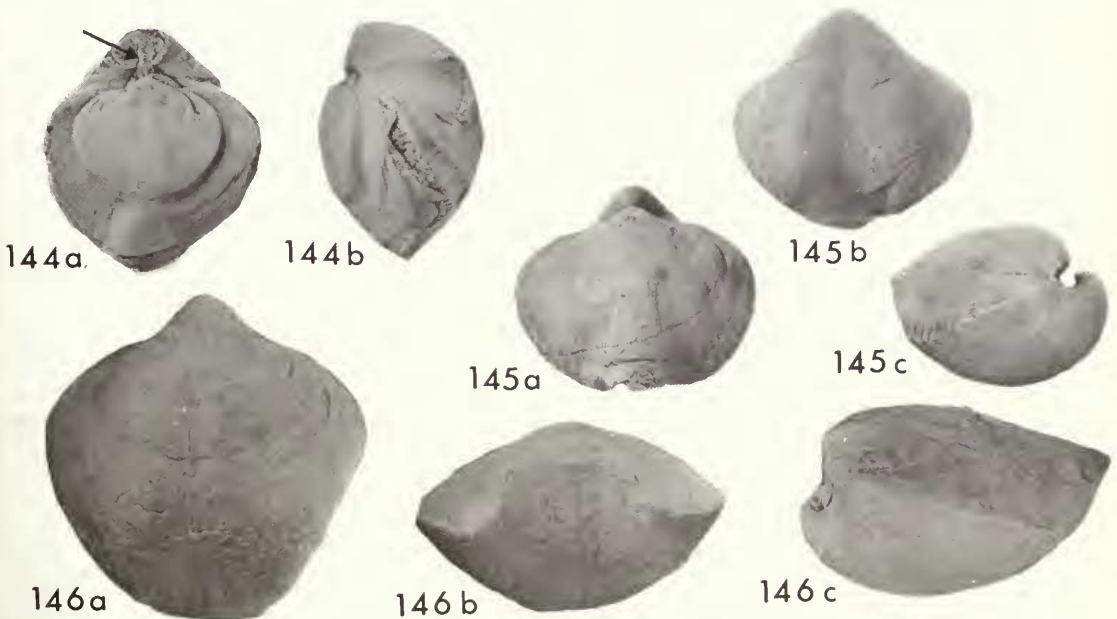
TYPE SPECIES. *Martina (Merospirifer) insolita* Reed 1949: 467, by original designation of Reed (1949: 470).

DIAGNOSIS. Martiniidae with broadly obovate outline and rounded transversely rhombic lateral profile. Indistinct ribs developed late in ontogeny. Dental plates subparallel and close to mid-line, crural plates lacking.

DISCUSSION. In 1949 Reed described two species under his new subgenus *Merospirifer*, *M. insolita*, which he stated (1949: 470) to be the type species of his subgenus, and *M. disparilis*; both came from the Charleston Main Limestone of Roscobie, Fife, of high Viséan (P_2) age. The material described by Reed is in the J. Wright Collection of the Royal Scottish Museum, Edinburgh. There are five syntypes of *M. insolita*, but, as Reed (1949: 468) remarked, that numbered 538 is the best specimen and is here selected **lectotype**. This specimen was figured by Reed (1949: pl. 10, figs 6–8) and is refigured here (Figs 146a–c).

Reed gave no separate subgeneric diagnosis but included doubtfully within *Merospirifer* the species *Martinia rhomboidalis* M'Coy, *Martinia galataea* Bell and *M. thetis* Bell. In addition the species *Spirifera linguifera* Phillips should belong to *Merospirifer* and it is to this species that certain poorly-preserved rare specimens from Fermanagh are assigned. *Merospirifer* was recognized as a genus in the Brachiopoda *Treatise* (Williams *et al.* 1965).

Within the Martiniidae the only established genera of Carboniferous age possessing dental plates are *Eomartiniopsis* and *Martiniopsis*, both of which appear to have crural plates, and



Figs 144–145 *Merospirifer linguifera* (Phillips). Fig. 144a, b, paralectotype, from the Viséan of Bolland, Yorkshire, viewed dorsally and laterally, showing a dental plate (arrowed) at the broken umbo; the specimen was damaged in life and grew in a distorted fashion. Figured by Phillips (1836: pl. 10, fig. 4). B248, $\times 1$. Fig. 145a–c, **lectotype**, here selected, from the Viséan of Bolland, Yorkshire, viewed dorsally, ventrally and laterally. BB61414, $\times 1$.

Fig. 146 *Merospirifer insolita* Reed. **Lectotype**, here selected, of type species of *Merospirifer*. From the late Viséan of Fife, Scotland, viewed ventrally, anteriorly and laterally. J. Wright Collection, Royal Scottish Museum, Edinburgh, no. 538, $\times 1$.

Martiniella and *Merospirifer* which lack crural plates, but are poorly known through inadequate original descriptions or illustrations. The weak development of ribs and shell outline seem to be characteristic of *Merospirifer*. *Martiniella* Grabau & Tien is described no more fully by Grabau (1931: 420) than by Williams *et al.* (1965) and it is difficult to know whether or not it is synonymous with *Merospirifer* or indeed *Eomartiniopsis* as suggested by Sokolskaya (1941) and Havlíček (1959). In the original description of *Crassumbo* Carter (1967), a member of the Reticulariidae, the genus was distinguished from *Eomartiniopsis* by having strongly thickened umbones. Roberts (1971), in describing *Crassumbo* ? *jonesi* from the Lower Carboniferous of the Bonaparte Gulf Basin of north-western Australia, compared it with *Martinia rhomboidalis* M'Coy, but is in error in calling it '*Spirifer rhomboidea* Phillips'. Phillips' (1836) species was not the same as that figured by M'Coy (1844: pl. 22 fig. 11); the former should be assigned to *Fusella* and the latter, as suggested by Reed, might belong to *Merospirifer*.

The geographical and stratigraphical range of *Merospirifer* is difficult to determine owing to the uncertainty of its recognition and relationships with similar genera. In the British Isles it ranges throughout the complete Viséan succession. The name has not been used outside the British Isles and the most closely related species would seem to be of Tournaisian age.

***Merospirifer linguifera* (Phillips)**

Figs 144, 145, 147–149

v* 1836 *Spirifera linguifera* Phillips: 219; pl. 10, fig. 4.

1859 *Spirifera glabra* var. *linguifera* Phillips; Davidson: pl. 12, figs 4, 5.

LECTOTYPE. Here selected, *Spirifera linguifera* Phillips from Bolland, Yorkshire, in the Gilbertson Collection of the BM(NH), BB61414 (Fig. 145).

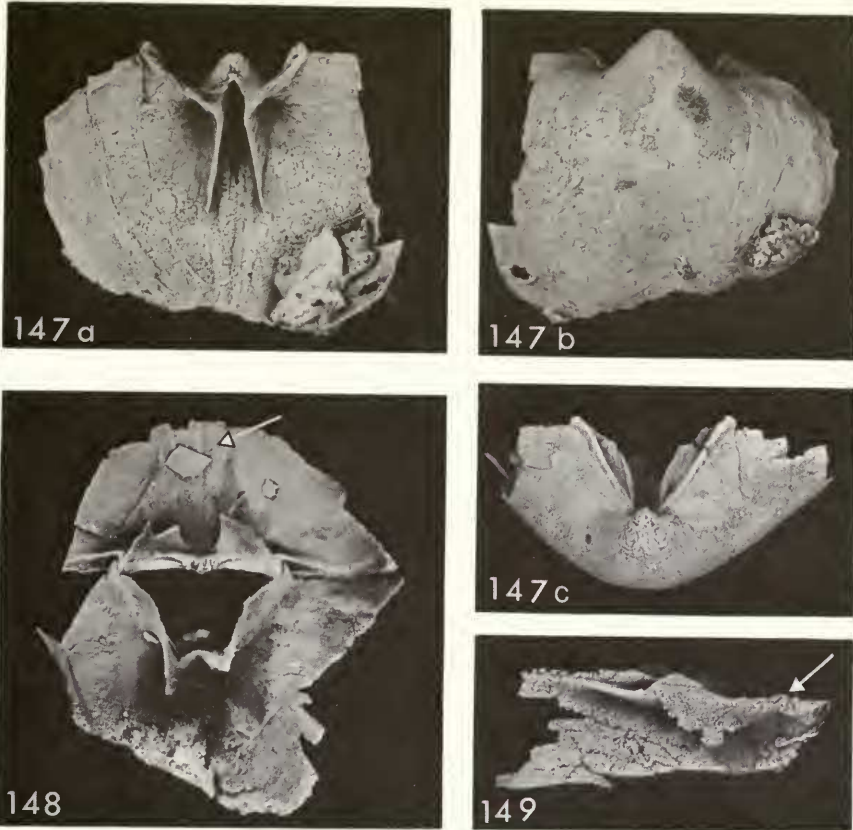
DIAGNOSIS. Relatively wide *Merospirifer* with seven to eight weak ribs on each flank. Ventral adductor muscle scars slightly elevated.

DISCUSSION. The species is represented in the Fermanagh fauna by only six incomplete ventral valves, a pair of articulated umbones (Fig. 148), and fragments. The longitudinally striated cardinal process and virtually smooth exterior places the material within the Martiniidae and the strong dental plates (Fig. 147a) and weak ribbing indicate assignment to *Merospirifer*. Although the Fermanagh specimens are insufficiently complete to determine their outline or profile, the relationship of their umbones, characteristics of the interareas and development of the ventral median sulcus are features closely comparable to those of Phillips' types of *M. linguifera*.

In the Gilbertson Collection of the BM(NH) there are five specimens labelled *linguifera*, two large and three small. One of the large specimens (B248) was figured by Phillips (1836: pl. 10, fig. 4) but is unfortunately somewhat atypical in that the shell is distorted into strongly developed concentric ridges, probably resulting from shell damage (Fig. 144). This specimen also has a broken ventral umbo. The second adult specimen (BB61414) is in good condition and, although not originally figured by Phillips, is the one selected above as lectotype of the species (Fig. 145). Both specimens were figured by Davidson (1859: pl. 12), but he restored the broken specimen and accentuated the ribbing so that the figures are poor representations of the originals.

Phillips' locality is Bolland and the species is quite common in the low Viséan (C₂S₁) mud-bank ('reef') facies of Clitheroe, Lancashire, a few miles east of the true Bolland localities. The same or a very similar species is also to be found in the higher Viséan (D Zone) 'reef' limestones of Staffordshire. These specimens differ from the Scottish material described by Reed in remaining smaller yet being relatively thicker. *M. insolita* also differs in being a relatively larger species than *M. linguifera*.

At the time when Reed described *Merospirifer* the term 'punctuation' was used in describing reticulariacean brachiopods; *M. disparilis* Reed was described as perhaps having a punctate shell substance. The term was used in describing the external micro-ornamentation of fine pits found on many of these shells, as well as the shell structural features we now know as endopunctuation and pseudopunctuation. In 1956 Williams used the term exopuncta in describing



Figs 147–149 *Merospirifer linguifera* (Phillips) from Co. Fermanagh. Fig. 147a–c, incomplete ventral valve, interior, exterior and posterior view; note the convergent dental plates below the delthyrial margins before they bend ventrally and diverge slightly to the valve floor. BB63691, $\times 2$. Fig. 148, conjoined umbones viewed internally showing the cardinalia (but with broken crura), articulation and broken dental plates; the dorsal adductor muscle scars can be seen (arrowed). BB63692, $\times 5$. Fig. 149, fragment of dorsal valve showing the socket, inner socket ridge and cardinal process (arrowed). BB63693, $\times 5$.

superficial pits penetrating no more than the primary shell layer, i.e. a form of external micro-ornamentation. Although some *Merospirifer* species may be slightly exopunctate, none is endopunctate.

Family ELYTHIDAE Frederiks 1919 (1924)

Genus *PHRICODOTHYRIS* George 1932

TYPE SPECIES. *P. lucerna* George 1932: 546; pl. 35, figs 2a–d; by original designation. Holotype in the Burrows Collection, Sedgwick Museum (No. 371), from the Viséan (D₂) of Lowick, Northumberland.

DISCUSSION. George fully described the genus in 1932 and besides the type species described five new species, *P. ericus*, *P. insolita*, *P. paricosta*, *P. periculosa* and *P. verecunda*. He redescribed the species *Terebratula* ? *lineata* J. Sowerby (1822: pl. 335, figs 1, 2; see Muir-Wood 1951: 105) and assigned it also to his genus, but it has since been made the type species of *Martinothyris* Minato 1953 on account of its dental and crural plates. In 1971 Thomas, following Maxwell's lead (1961), called into question the validity of *Martinothyris* because Muir-Wood (1951)

had suggested that *P. lineata* (J. Sowerby), with lectotype no. B60997 in the Sowerby Collection, BM(NH), lacked dental plates. This then contradicted the characteristic feature, the presence of dental plates, by which Minato separated his genus from *Phricodothyris*. On this basis Thomas (1971) correctly concluded that George's (1932) specimen assigned to *lineata* did not belong to that species and consequently that *Martinothyris* was invalid.

While discussing the specimens illustrated by Sowerby, Muir-Wood (1951: 105) wrote that there was an 'apparent absence of apical plates.' However, careful inspection of the lectotype shows reasonably conclusively that there are dental plates, and possibly also short crural plates, as illustrated by George (1932: fig. 6) in a specimen from Treak Cliff, Derbyshire. Thus, although the Sowerby specimen of *lineata* invalidates George's neotype it supports the description he gave of this species which was used by Minato in describing *Martinothyris*. There is, therefore, both a valid type species for this genus and a valid lectotype of that species.

The type specimens of all George's five species came from D Zone rocks of northern England or Scotland and were characterized by outline, whether transverse, equidimensional or elongate; the form of the anterior commissure; the degree of biconvexity; and the spacing of the spine-bearing lamellae. Unfortunately, there is insufficient well-localized material to test the validity of these species, but observations support George's work. The genus is represented in low Viséan rocks and extends into the Permian where the characteristic barbed spines have been beautifully illustrated on Bolivian specimens (Samtleben 1971).

Minato (1953; see also Minato & Kato 1963) erected the genus *Nebenothyris*, based upon *Spirifer* (*Reticularia*) *lineata* Nebe (*non* Martin), characterized by possessing 'a prominent median septum in the ventral valve . . . and a septum in the dorsal valve.' Otherwise *Nebenothyris* was said to resemble *Phricodothyris*. The true nature of specimens within this group having at least a low ventral median ridge is being investigated in an attempt to check the validity of *Nebenothyris*. Until that study is complete, and despite the low ventral ridge in the Fermanagh specimens, I retain their position in *Phricodothyris*.

Phricodothyris verecunda George

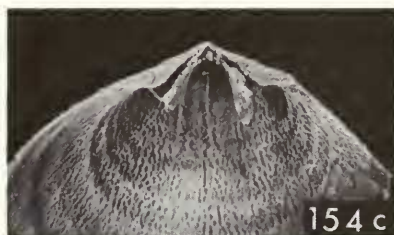
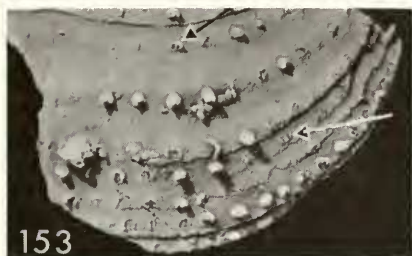
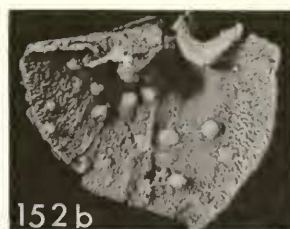
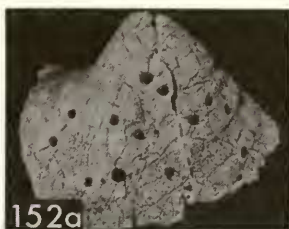
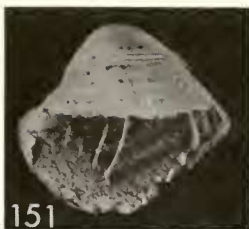
Figs 150–159

HOLOTYPE. A specimen from the D₂ zone (Brachiopod Beds) of Chrome Hill, Derbyshire, in the P. Roscoe collection of the BM(NH), B46709. Figured by George (1932: pl. 35, figs 3a–d).

DIAGNOSIS (George 1932). An equidimensional biconvex rectimarginate form, in which the spine-bearing growth-halts are regularly distributed over the surface.

DESCRIPTION. George's original description seems to have been based only upon the holotype. The Fermanagh silicified material came principally from the Sillees river locality and comprises six shells plus numerous incomplete dorsal and ventral valves. This material is assigned to *P. verecunda* on account of its equidimensional outline, strongly biconvex lateral profile with a

Figs 150–159 *Phricodothyris verecunda* George, from Co. Fermanagh. Fig. 150, juvenile dorsal valve interior showing the young inner socket ridges and one crus; the valve is bored. BB63441, $\times 7$. Fig. 151, incomplete young shell viewed anterolaterally, showing parts of the spiralia. BB63442, $\times 4$. Fig. 152a, b, incomplete young, highly bored, ventral valve exterior and interior to show the 'blisters' of shell repair on the inner surface. BB63443, $\times 4$. Fig. 153, part of dorsal valve exterior showing the typical spinose ornamentation of the genus; the upper and lower arrows indicate the different appearances of the 'spine' bases according to the degree of abrasion. BB63444, $\times 4$. Fig. 154a–c, incomplete dorsal valve viewed externally, showing ornamentation, and internally, $\times 4$, and detail of the cardinalia, $\times 6$. Note also the characteristic internal ornamentation. BB63440. Fig. 155a, b, incomplete ventral valve interior, showing dental ridges and median ridge, $\times 4$, and posteriorly, showing the small interarea and ridges at the delthyrial margins, $\times 6$. BB63438. Fig. 156, conjoined umbones showing the valve articulation. BB63439, $\times 4$. Fig. 157, lateral view of complete shell. BB63436, $\times 1.5$. Fig. 158a, b, an almost complete shell viewed ventrally, $\times 2.5$, and obliquely illustrating the delthyrial region, $\times 5$, showing the external ornamentation. BB63437. Fig. 159, almost complete shell viewed posterodorsally. BB63436, $\times 3.5$.



prominent ventral umbo, and rectimarginate anterior commissure. The external ornamentation differs from that of the holotype, in which George records 14–16 growth lamellae in a length of 10 mm. The frequency of spine-bearing growth lamellae in the Fermanagh specimens varies considerably according to position on the shell and the size of the shell. Posteriorly and again on some individuals marginally, these lamellae are more crowded than over the anteromedian sectors of the valves, where 7–11 lamellae occur in a length of 10 mm. Similarly the lateral frequency of spine-bases on any one lamina varies (compare Fig. 153 with Fig. 158b). The holotype has an eroded surface but has 35 to 40 spine bases in a width of 10 mm. On the Fermanagh shells the frequency varies from 11 to 25 in 10 mm width.

The interiors of valves more than about 10 mm wide are marked, especially posteriorly, by a characteristic pitting (Figs 154b, 155a), which in areas of muscle attachment is modified to a series of sinuous elongate grooves. The ventral valve is aseptate, the teeth being supported only by dental ridges and a low median ridge never developed to more than a fraction of a mm in height (Fig. 155a). Within the dorsal valve the sockets are floored by horizontal fulcral plates extending from the valve walls to the dorsally slightly convergent crura (Fig. 154b, c). These are unsupported and poorly differentiated from the inner socket ridges. The diductor muscle attachment area is apical, small and typically spiriferide in being longitudinally striate or tuberculate (Fig. 156). The dorsal adductor muscle scars are separated by a low ridge which is persistent throughout ontogeny, and in older valves the lateral margins of the scars are confined by a pair of similar low ridges.

DISCUSSION. Valves down to a width of about 2.5 mm can be recognized easily. At this size dorsal valves have an indistinct median ridge extending almost to the anterior margin; the diductor muscle attachment area is indistinguishable (Fig. 150). The inner socket ridges diverge at about 90° from each other in juvenile valves and only increase their angle of divergence to about 100° in the oldest observed valves. The ridges lateral to the adductor scars are visible in valves 9.0 mm wide and from then on became more prominent.

Ventral valves are devoid of any strongly developed morphological features and it is difficult to recognize any ontogenetic changes other than the above-mentioned pitting of the internal surface and greater prominence of the median ridge in old shells. The muscle scars are ill-defined even in the large valves, but it seems that the adductor scars are narrowly ovate and flanked by rounded triangular diductor scars extending anteriorly for just over half the valve length. At their widest point, anteriorly, the diductor scars are about one-third of the total valve width.

The evidence from the silicified specimens indicates that the delthyrium remained open throughout life (Fig. 158b, 159), in which case the pedicle may have remained functional as the principal means of attachment to the substrate. If so, the lack of abrasion at the umbones indicates that the substrate was probably soft and, as George (1932) pointed out, the spine morphology would appear to be suited to function as anchors within the sediment. However, the examination of conjoined umbones shows that the greater part of the delthyrial opening would have been blocked by the dorsal umbo when the shell was open (Fig. 156). The maximum angle through which the shell could have opened is dictated by the disposition of the dorsal and ventral interareas and this varies from 25° to 40°. If in life the gape was of about 30° this would have brought the dorsal umbo into the delthyrial opening, leaving only a few tenths of 1 mm apically through which a pedicle might have emerged. Thus although the species was probably attached by the pedicle when young it seems likely that older shells, provided with barbed spines, relied upon these to 'hold' into the sediment. This corona of spines, extending well beyond the margins of the shell, could also have inhibited predation. If so it appears to have been reasonably successful in that only two specimens in about 50 have been bored. This compares with 30% to 50% of the valves of some relatively smooth productacean and chonetacean species from the same fauna (Brunton 1966a). The two specimens of *P. verecunda* which are bored are illustrated; the hole in the juvenile dorsal valve (Fig. 150) resembles those thought to have been produced by carnivorous gastropods. The holes in the old ventral umbo (Fig. 152) resemble those produced in some living shells by the boring sponge *Cliona*. Dr D. George (BM(NH), Dept. of Zoology) suggests to me that the burrowing polychaete *Polydora* would be expected to

produce less circular, more elongate or dumbbell-shaped burrows in the shell. These borings were for habitation and the living brachiopod reacted to the boring by depositing pustules of shell internally (Fig. 152b). Externally the holes are about 0.3 mm in diameter, circular and may have somewhat bevelled edges. In some instances it appears that the cavity within the pustule of shell is slightly larger than the opening at the original shell surface. The minute branching infestation of burrows on the outer surface (Fig. 152a) are those I previously (1966a) thought to have been made by ctenostome bryozoans. More recently work by Voigt (1975) indicates that the ichnogenus *Talpina*, resembling these burrows, resulted from the activities of phoronids.

Family VERNEULIIDAE nov.

DIAGNOSIS. Transverse to subcircular spiriferaceans with equibiconvex profiles. Opposite folding forming ligate to metacarinat anterior margins. Ventral interarea narrow to full width of shell, with open delthyrium or apically restricted by a deltidium. A pair of prominent costae bordering the median sulci, with or without a pair of weaker lateral costae. Micro-ornament apparently of growth lines only. Spiralia laterally directed. Shell substance impunctate.

DISCUSSION. The family includes the genera *Verneulia* Hall & Clarke, 1894 and *Minythyra* nov., and ranges from mid-Devonian through the Lower Carboniferous.

Verneulia was not placed in a family in the *Treatise* (Williams *et al.* 1965) and remains a poorly known genus. The type species, *Spirifer cheiropteryx* d'Archaic & de Verneuil 1842, came from the mid-Devonian of Germany, but the name originally also included specimens from the Carboniferous of Visé, Belgium. These specimens were separated as *S. oceani* by d'Orbigny (1850), leaving the much wider Devonian form for the type species. *Verneulia oceani* is a rare species, seldom if ever figured since de Koninck (1887). One of the three specimens in the Davidson Collection of the BM(NH), B7923, from the type area of Visé, Belgium, is here selected as **neotype** (Fig. 160).

The impunctate shell and spiralia place the family in the Spiriferacea. The development of a persistent ventral interarea precludes the possibility of these genera being assigned to the Athyrididae, although from their outline shapes they resemble some athyrids. The unusual shapes and opposite folding also resembles some Mesozoic zeilleriid terebratulids, such as *Cheirothyris* or some *Zeilleria* species, and it seems that the shape is one that has been repeated occasionally during the evolution of brachiopods in otherwise unrelated stocks.

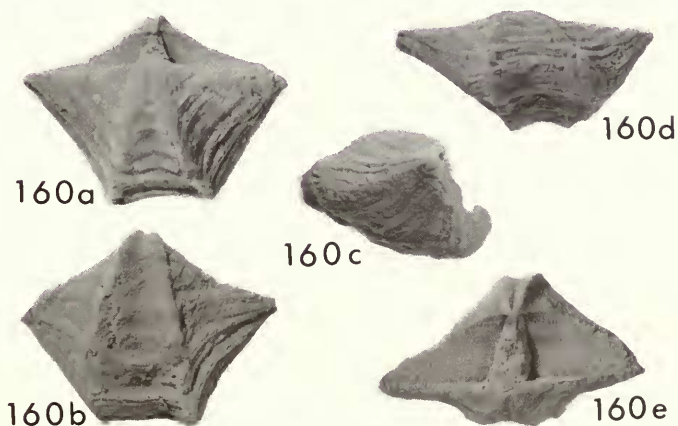


Fig. 160 *Verneulia oceani* (d'Orbigny). Dorsal, ventral, lateral, anterior and posterior views of the **neotype**, here selected, from the Viséan of Visé, Belgium; Davidson Collection. The specimen closely resembles the illustrations of the species de Koninck (1887) and this is probably the first time the species has been photographically illustrated. B7923, $\times 3$.

Verneuilia has a wide, high ventral interarea which, at least in *V. oceani*, has the vertically disposed microcrenulations in the shell material commonly described as a fine denticulation, and typical of many spiriferaceans. The delthyrium is closed apically by a short deltidium, but the genus remains unknown internally.

Genus *MINYTHYRA* nov.

TYPE SPECIES. *Minythyra loph*a sp. nov.

DIAGNOSIS. Minute, subcircular, equibiconvex spiriferids. Both valves with prominent median sulci, bordered by strong ridges (costae), less distinct costae on flanks. Open delthyrium in apsacline interarea. Hinge line up to one half full shell width. Micro-ornament lacking. Laterally directed spiralia, no median septum. Shell impunctate.

NAME. Greek, *μινύς* = little or small, + *θύρα* = door. Fem.

DISCUSSION. The minute shells, from the silicified fauna, assigned to this genus cannot be considered as the young of any other species in the fauna. Externally *M. loph*a sp. nov. might be thought similar to the young of *Hustedia ulothrix*, but that species is distinct in being endopunctate and in having an apical pedicle foramen.

The impunctate shell and spiralia place the genus in the Spiriferida. The external outline is reminiscent of the young of some Devonian athyrid genera, such as *Anathyris* and *Pradoia*, or of the Carboniferous genus *Verneuilia*, with which I place *Minythyra* in the Verneuiliidae. *Verneuilia* is characterized by similar median sulci and bordering costae to *Minthyra*, but differs in having a very broad hinge line, forming much the widest part of the shell, a wide and high ventral interarea, and no flanking costae.

In addition to the type species I assign *M. ernea* sp. nov. and *Rhynchonella opposita* White & Whitfield 1862 (Figured by Weller, 1914: pl. 82, figs 11–13, as *Composita opposita*) from late Kinderhook beds of Iowa, U.S.A., to *Minythyra*.

*Minythyra loph*a sp. nov.

Figs 161–168

DIAGNOSIS. *Minythyra* with a metacarinat outline resulting from strong costae bordering median sulci, plus a weaker pair of flanking costae.

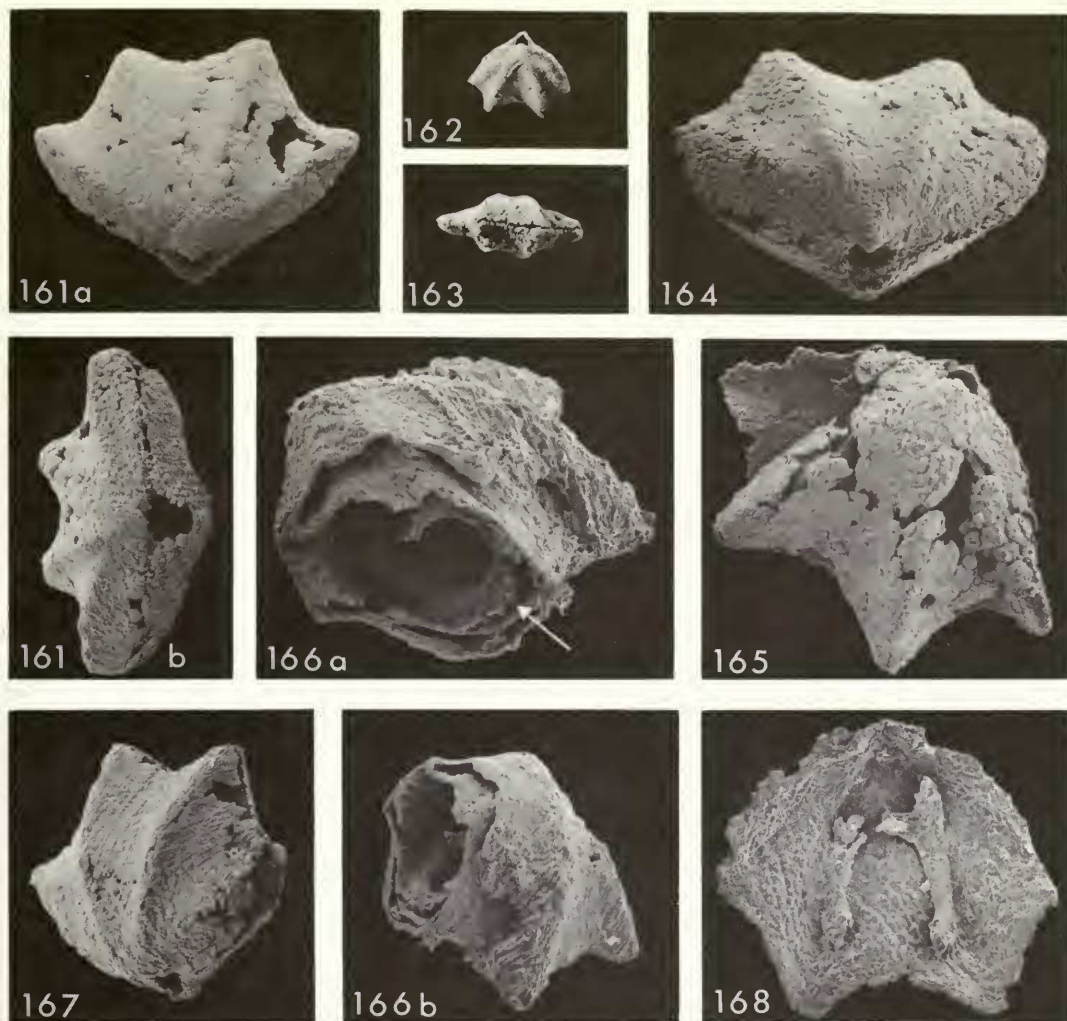
NAME. Greek, *λόφος* = crest or ridge, referring to the strong costae.

LOCALITY. Sillees River.

HOLOTYPE. BM(NH) specimen no. BD147, figured here as Figs 161a, b.

MATERIAL. The holotype plus 40 other complete and incomplete silicified specimens, BB65054–BB65063 and BD135–BD149. Length range from 0.8 mm to 1.2 mm.

DESCRIPTION. Minute, transverse and strongly emarginate shells reaching 2 mm wide and 1.2 mm long. The valves have opposed folding, forming a metacarinat outline and anterior margin (Williams *et al.* 1965: H63) (Figs 162, 163). The costae bordering the median sulci are stronger than the flanking pair. The profile is equibiconvex with an apsacline ventral umbo extending beyond the low anacline dorsal umbo (Fig. 167). An open delthyrium is set in the interarea which extends to approximately one-third of the maximum shell width. The exteriors lack surface ornamentation or growth lines. Internally the only distinguishable features are the teeth, sockets and traces of spiralia (Fig. 166). The teeth are short, but relatively broad knobs protrude from the dorsal corners of the delthyrium. These fit against stout thickenings of the dorsal hinge line, on each side of the umbo, which extend anteroventrally as low inner socket ridges (Fig. 168). (For discussion see below.)



Figs 161–168 *Minythyra lophata* gen. et sp. nov., from Co. Fermanagh. Fig. 161a, b, **holotype**, posterodorsal and posterior views. BD147, S.E.M. $\times 20$. Fig. 162, dorsal view of complete specimen. BD137, $\times 7$. Fig. 163, posterior view of complete specimen. BD135, $\times 7$. Fig. 164, posterodorsal view of complete specimen. BD144, S.E.M. $\times 28$. Fig. 165, dorsal view of incomplete shell. BD141, S.E.M. $\times 27$. Fig. 166a, b, incomplete shell seen laterally, S.E.M. $\times 29$, and anterolaterally, S.E.M. $\times 22$; the ventral valve is uppermost and part of a spiralium can be seen on which spinose outgrowths (arrowed) developed on the anterior part of the whorls. BD145. Fig. 167, shell viewed dorsolaterally. BD142, S.E.M. $\times 21$. Fig. 168, dorsal valve interior showing shallow sockets (arrowed) and initial sections of the spiralia, including the incomplete jugum; the silica of the internal surface appears to have replicated a mosaic of secondary shell fibres. BD146, S.E.M. $\times 26$.

Minythyra ernea sp. nov.

Figs 169, 170

DIAGNOSIS. *Minythyra* with subcircular outline and narrow ventral interarea. The costation is weak.

NAME. From Lough Erne, Co. Fermanagh, in the region from which the specimens were collected.

LOCALITY. Sillees River.

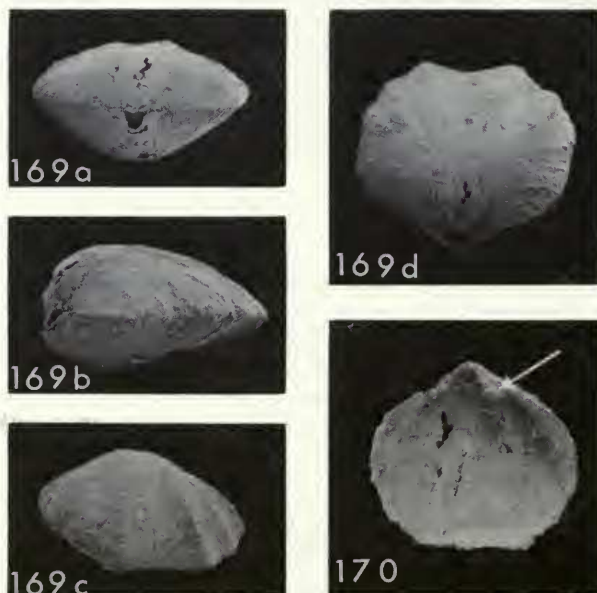
HOLOTYPE. BM(NH) specimen no. BD133, figured here as Fig. 169a–d.

MATERIAL. The holotype plus 20 other specimens, BD99–BD108 and BD125–BD134. Length range from 1.1 mm to 1.8 mm.

DESCRIPTION. Outline subcircular to transversely broadly elliptical with a weakly bilobate anterior commissure. Profile is equibiconvex, with a narrow apsacline ventral interarea, mostly occupied by the delthyrium. The median sulci and bordering costae are weakly developed. On the flanks a second pair of faint costae are positioned anterior to the place of maximum width. Articulation is by knob-like teeth (Fig. 170) and sockets.

DISCUSSION. The two species of *Minythyra* in the silicified faunas are similarly sized, but readily distinguished by the strongly trisinate outline and strongly developed costae in *M. lophia*, as compared to the more rounded outline and weak costation in *M. ernea*. The Kinderhookian (Tournaisian), North American species *M. opposita* (White & Whitfield) is unknown internally, but belongs here more happily than in *Composita*, to which it was assigned by Weller (1914). It is a trisinate shell anteriorly, with costation similar to *M. lophia*, but posteriorly the umbonal angle is not more than 100° , while that of *M. lophia* is in the range of 110° to 120° . It would seem that the North American species has a narrow hinge line, since an interarea is not described, despite the shell dimensions reaching 5.5 mm long and 6.0 mm wide (Weller 1914).

One must always have doubts whether small specimens such as these are valid as true species, and not to be interpreted as the young of other species. However, until a species is found to which these shells can be assigned it is more practical to consider them as independent taxa. While the possibility exists that the young from a recently arrived spat fall, of a hitherto unknown species, might have been entombed in the area, the known presence of minute species of brachiopods in the fossil record and in modern seas makes the likelihood of these specimens representing distinct species all the greater. In Recent British waters species of *Argyrotheca* and *Gwynia* reach only a few mm in length when fully grown.



Figs 169–170 *Minythyra ernea* gen. et sp. nov., from Co. Fermanagh. Fig. 169a–d, holotype, posterior, lateral, anterodorsal and dorsal views; the small ventral interarea can be seen, but the medial lineations may be a replication of shell fabric rather than original ornamentation. BD133, S.E.M. $\times 20$. Fig. 170, inside of ventral valve showing a tooth (arrowed). BD134, S.E.M. $\times 20$.

The absence of distinguishable growth lines on these Fermanagh species, despite their preservation on other species, indicates that *M. loph*a and *M. ernea* are young, in the sense that they have not experienced the shell growth halts seen on most larger shells. However, in the fauna as a whole some species, such as the externally rather smooth *Crurithyris urei*, show few growth lines until several mm in length while, by contrast, specimens of the lamellose *Cleiothyridina fimbriata* show many growth lines from a length of about 0.5 mm. Thus both speed of shell growth and external ornamentation have to be considered in the question of the state of maturity or age of *Minythyra* specimens. Since species of *Crurithyris* and *Nucleospira* display occasional growth lines at shell lengths of less than 1 mm, whereas *Minythyra* species do not, it seems that the latter may have grown rapidly to their preserved size within a single growth season. The consistent small size and small total number of specimens recovered from the acid-developed blocks is suggestive of a single assemblage in the area, as distinct from an established population persisting through the time of deposition of the limestone bed from which they came.

Order TEREBRATULIDA Waagen 1883

Despite the classical works of Cloud (1942) on Silurian and Devonian terebratulids, Campbell (1965) on Permian taxa, and of Stehli (1956, 1961, 1965), our knowledge of west European Lower Carboniferous species remains slight. Certain generic and specific names, such as *Dielasma hastata*, abound in the literature so widely that they now represent 'sack' taxa representing genera besides *Dielasma* (see Brunton 1982), and are in need of revision. The problem in the classification of these species is that the external shapes of several are very similar and only by studying internal structures can their true identity be recognized. Thus, from the typical limestones of the European Lower Carboniferous it is necessary to section specimens serially, or use acid-developed material, in order to demonstrate the nature of the cardinalia, the loop and presence of dental plates. Only then can correct generic assignments be made.

There is a generalization which may help to distinguish specimens of the short-looped Terebratulidina from the long-looped Terebratellidina which seems to hold good at least in the Carboniferous. When the loop cannot be seen, or is broken, it is noteworthy that taxa of the long-looped Cryptonellidae, the only Palaeozoic members of the suborder, have less incurved, straighter to suberect ventral umbones than do short-looped taxa. In addition the pedicle foramen tends to be more within the delthyrium than in short-looped forms and, at least in European Carboniferous species, the density of endopuncta is much greater in *Cryptonella* than in short-looped species.

Using the *Treatise* (Williams *et al.* 1965) classification it is possible to recognize four distinctive genera and species, three short-looped Dielasmataceans (*Girtyella*, *Alwynia* and *Beecheria*) and one long-looped Cryptonellacean (*Cryptonella*). Work by Dagys (1972) led him to reclassify terebratulids so that loop length was less important than the ontogeny and form of the cardinalia as a whole. From his studies Dagys suggested seven superfamilies in the Terebratulida, the Stringocephalacea, Cryptonellacea, Dielasmatacea, Terebratulacea, Dallinacea, Loboidothyraacea and Terebratellacea. Of these, Cryptonellacea and Dielasmatacea are present in the Carboniferous, where they include the following European genera:

Cryptonellacea:

Cryptonellidae
*Cryptonella**

Cranaenidae
*Girtyella**
Hartella

Notothyrididae
*Alwynia**

Dielasmatacea:

Dielasmatidae
'*Dielasma*'
Balanoconcha

Heterelasminidae
*Beecheria**

*Present in this Fermanagh fauna.

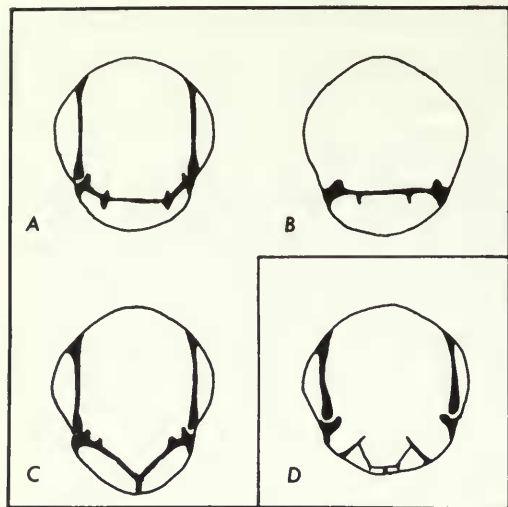


Fig. 171 Stylized cross sections of *Cryptonella* (A), *Alwynia* (B), *Girtyella* (C) and *Beecheria* (D); A–C are cruronellaceans while D is a dielasmatacean. Ventral valves are drawn uppermost. The sections illustrate the differences in the disposition of the crural bases to the outer and inner hinge plates – they project dorsally and ventrally in *Cryptonella*, dorsally in *Alwynia* and ventrally in *Girtyella*. In *Beecheria* the crural bases are supported by thickened outer hinge plates, the inner hinge plates forming an almost sessile septalium containing muscle scars.

In this classification Dagys (1972) unites those Carboniferous genera which in adulthood have entire hinge plates, free of the valve floor, other than for a connection by a median septum (see Fig. 171A–C). The dielasmatacean genera have hinge plates which join to the valve floor, tending to diverge anteromedially, leaving the middle of the valve floor free (Fig. 171D). Thus the Dagys (1972) classification seems to have merit and although amongst the Carboniferous genera the long-looped *Cryptonella* stands out from the rest in having about 450 endopuncta per mm^2 as compared to 100–250 per mm^2 in the short-looped forms, this characteristic may be more closely related to ecology than to supraspecific classification. Foster (1974) has shown that amongst living Antarctic brachiopods different species of the same genus may have varied punctal densities. He followed Campbell (1965) in suggesting that species from warm waters have more puncta per mm^2 than those from cold water, but also that greater depth may result in fewer puncta, despite the fact that warmer water occurred at depth in the Antarctic. The presence of different species in the Fermanagh samples with either high or low densities of puncta seems to contradict the idea that ecology is the most important factor controlling this feature and a full review of the punctal densities in terebratulids through time should be revealing.

In this faunal description I classify the species according to the work of Dagys (1972), which appears to be based on more sound principals than those of the *Treatise* (Williams *et al.* 1965). However, I use the terms for parts of the cardinalia more or less as in the *Treatise* and in Campbell (1965), as follows.

Outer hinge plates connect the crural bases to the inner socket ridges or valve floor laterally. *Inner hinge plates* lie medially of the crural bases, meeting medially on a median septum, or fusing to the valve floor medially.

Crural bases are those parts of the crura fused with the hinge plates and separating outer from inner hinge plates.

Differences between the *Treatise* and Campbell's definitions occur when a median trough-like structure (as in *Girtyella*) is present. Campbell (1965) argued for a purely descriptive definition and called the structure a septalium, composed of the inner hinge plates only, while the *Treatise* (Williams *et al.* 1965) added the functional criterion of adductor muscle attachment, reserving the term septalium only for the structure not carrying adductor muscles. In the *Treatise* such a structure, with adductor muscle attachment, would be termed a cruralium. The problems of interpreting function make this *Treatise* definition undesirable.

Johnson & Westbroek (1971) discussed this problem of terminology, concluding that when cardinalia contained both subhorizontal and ascending plates (forming a V or Y to the valve

floor) the terms inner hinge plates should be used for the former (subhorizontal structures) and crural plates for the latter. However, in terebratulids, where a double structure such as this is unknown, the distinction between crural bases or hinge plates remains problematical. It might be argued that the Y-shaped cardinalia of *Girtyella*, in section, are composed of crural plates converging to a median septum forming a septalium (*sensu* Johnson & Westbroek, 1971), or of inner hinge plates alone (*sensu* Campbell, 1965), or of inner hinge plates converging onto a median septum (*sensu* Williams *et al.*, 1965). The growth and role of the median septum is varied in terebratulides and I think it should not be critical to the use of the term septalium, which I restrict to the trough-like structure, supported or not by a median septum.

Superfamily **CRYPTONELLACEA** Thomson 1926

Family **CRYPTONELLIDAE** Thomson 1926

Genus **CRYPTONELLA** Hall 1861

REMARKS. Long-looped cryptonellids are seldom recorded from Carboniferous rocks of Europe, and the genus *Cryptonella* is externally similar to other short-looped genera such as *Cranaena* or *Dielasma*. If the loop is not preserved it can be difficult to distinguish long-looped species, but it may prove true that they are more densely endopunctate (*Cryptonella* having about 450 endopuncta per mm²), and that their ventral umbones are straighter, having less incurved pedicle apertures in a submesothyrid position.

Cloud (1942) restricted the genus to the Devonian but Stehli, in the *Treatise* (Williams *et al.* 1965), extended it up into the Permian. The type species, *C. rectirostra* (Hall), comes from the mid-Devonian of North America. Several cryptonellid genera are recorded from the Permian of south-west Texas by Cooper & Grant (1976), but not *Cryptonella* itself.

Cryptonella minranensis sp. nov.

Figs 172–183

1982 *Cryptonella* sp.; Brunton: figs 2, 3.

DESCRIPTION. Small *Cryptonella*, commonly less than 10 mm long, with the greatest width at about two-thirds of the length. Anterior margin is rounded and the commissure rectimarginate. In lateral profile the shell is equibiconvex with prominent growth steps and a nearly straight to suberect pedicle umbo, the aperture being mesothyridid (Fig. 172a). Dental plates are well developed (Fig. 178a). In the dorsal valve the hinge plate is perforated posteriorly, remaining horizontal and unsupported between the inner socket ridges (Figs 177, 183). The crural bases extend across the hinge plate, close to the inner socket ridges, as both dorsal and ventral ridges. Endopunctuation is dense and prominent, with about 450 endopuncta per mm².

NAME. From Minran Hill, 2 miles NNW of Derrygonnelly, Co. Fermanagh, adjacent to the type locality.

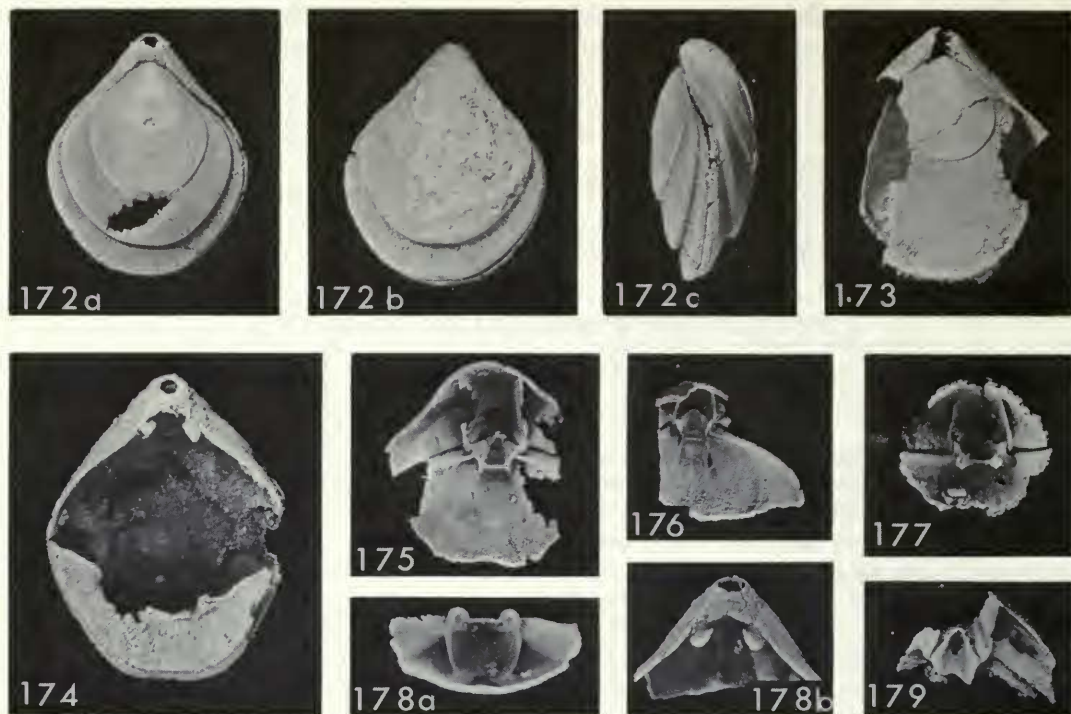
HOLOTYPE. BM(NH) specimen no BB64048; Fig. 172a–c.

LOCALITY. The type locality is collecting locality 14/4B, near Bunnahone Lough, Co. Fermanagh.

HORIZON. Asbian (D₁), Dinantian, Lower Carboniferous.

MATERIAL. About 140 specimens came from the type locality, 14/4B, below Minran Hill, near Bunnahone Lough: BB63166–BB63170, BB64030–BB64039, BB64048–BB64053, BD182–BD186. About 34 came from locality 14/4A at Carrick Lough: BB63986–BB63995, BB64023–BB64024. About 12 came from Milltown Bridge stream: BB63981–BB63985. Many of the specimens are fragmentary.

DISCUSSION. A diagnosis is not presented since other contemporary *Cryptonella* species are unknown. This is the most abundant of the four terebratulide species in the Fermanagh



Figs 172–179 *Cryptonella minranensis* sp. nov., from Co. Fermanagh. Fig. 172a–c, **holotype** viewed dorsally, ventrally and laterally; note the exposed deltidial plates and straight ventral umbo. BB64048, $\times 7$. Fig. 173, dorsal view of incomplete shell (viewed stereoscopically in Fig. 180), from Carrick Lough. BB64023, $\times 8$. Fig. 174, dorsal view of ventral valve showing the teeth. BB64049, $\times 6$. Fig. 175, conjoined umbones viewed internally to show articulation, the cardinalia and crural bases (arrowed). BB64051, $\times 7$. Fig. 176, conjoined umbones showing the cardinalia and crura. BB64052, $\times 2$. Fig. 177, conjoined umbones viewed internally showing the articulation and unsupported hinge plates; from Carrick Lough. BB60024, $\times 10$. Fig. 178a, b, ventral valve umbo viewed internally and dorsally showing the teeth and deltidial plates. BB64050, $\times 7$. Fig. 179, internal view of a dorsal umbo, plus half the ventral umbo, showing the posteriorly perforate hinge plate. BB64053, $\times 7$.

acid-developed faunas. The external shape can be confused most easily with *Girtyella carrickensis* sp. nov. (p. 110), but *C. minranensis* is relatively wider and has a suberect ventral umbo, leaving the deltidial plates exposed, as compared to the slightly incurved labiate beak of *G. carrickensis*. In addition the punctal density differs greatly; at about 450 puncta per mm² it is almost twice that of *G. carrickensis*. The dorsal valve cardinalia are quite different, but those of *Cryptonella* species are like those of *Alwynia* species, which can however be easily separated by the lack of dental plates, as in *A. reidi* sp. nov. (p. 114).

The strong development of growth halts, forming steps in the lateral profile of the shell, may not be characteristic of the species. The other three species also have some prominently-developed growth halts, so it is likely that these resulted from environmental factors rather than genetic control.

There are a few young specimens in the fauna in which brachial loops are preserved. These show that at a brachial valve length of about 4 mm there is an early cryptacanthiiform loop almost 3 mm long (Figs 180, 182). This juvenile loop has descending branches uniting anteromedially as an echmidium. At the median line of junction a vertical plate extends anteriorly, with a spinose serrated edge (Fig. 182b), and ventrally approaches close to the ventral valve. At this stage the ventral end of the median plate has a pair of lateral extensions

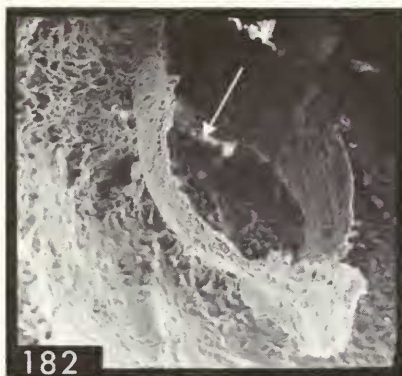


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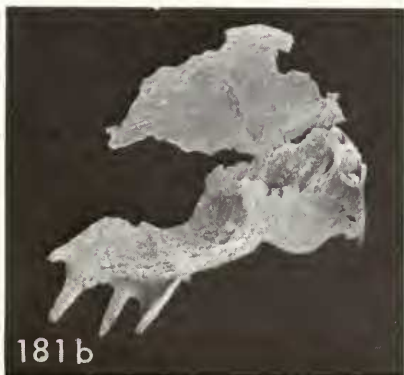
Fig. 180 *Cryptonella minranensis* sp. nov. Stereoscopic pair of an incomplete shell from Carrick Lough, viewed laterally to show the immature (cryptacanthiiform) brachial loop inside. BB64023, $\times 4$; see also Fig. 173.



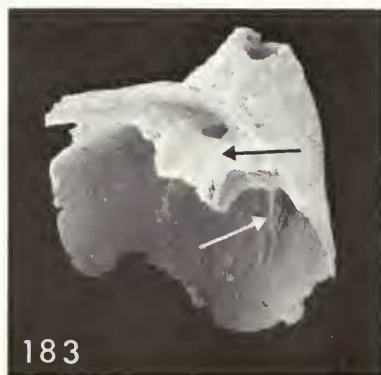
181a



182



181b



183

Figs 181–183 *Cryptonella minranensis* sp. nov., from Co. Fermanagh. Fig. 181a, b, brachial loop, with cardinalia and part of the ventral umbo, viewed ventrally and anterolaterally; one preserved dental plate and the hinge plate perforation are arrowed. BD182, S.E.M. $\times 15$. Fig. 182, simple juvenile loop; the anterior edge of the hinge plate is arrowed. BD183, S.E.M. $\times 60$. Fig. 183, conjoined umbones showing the underside of the perforate hinge plate, with ridges of the crural bases and one of the dental plates (both arrowed). BD184, S.E.M. $\times 15$.

representing either an early stage in the development of the hood or the remnants of a broken hood. At this stage of development the loop is very similar to that described by Cooper & Grant (1976) in Permian *Cryptonellidae*.

Of the many terebratulide species described by de Koninck (1887) from the Carboniferous of Belgium, two externally resemble *Cryptonella* in appearing to have relatively straight to suberect ventral umbones. These are *Dielasma amygdaloides* de Koninck (1887: pl. 4, figs 26–40) and *D. subfusiforme* de Koninck (1887: pl. 5, figs 32–44). Of these, the former is somewhat more similar to *C. minranensis*, but without a knowledge of their interiors it is impossible to assign these de Koninck species accurately.

Family CRANAENIDAE Cloud 1942
Subfamily GIRTYELLINAE Stehli 1965
Genus *GIRTYELLA* Weller 1911

Weller first described the genus (1911: 442), with *Hattinia indianensis* Girty 1908 as type species. His sections of the type species clearly showed a concave hinge plate or septalium, supported from the umbo by a median septum. The *Treatise* (Williams *et al.* 1965) illustration (fig. 614.2b) is poor, showing the inner hinge plates as being too flat, while in fact they resemble more closely those of the Permian genus *Fletcherithyris* Campbell. Apart from any stratigraphical differentiation, *Girtyella* differs from *Fletcherithyris* in having a persistent dorsal median septum supporting the inner hinge plates, which, in *Fletcherithyris*, fuse to the valve floor and during growth anteriorly develop a median septum. Furthermore, Campbell (1965) points out that *Girtyella* has a medially-angled transverse band to its loop (lacking in his genus) and that the endopuncta of *Girtyella* have a density of about 280 per mm², as compared to 90 per mm² for *Fletcherithyris*.

Girtyella carrickensis sp. nov.
Figs 184–194

1982 *Girtyella* sp.; Brunton: fig. 4.

DIAGNOSIS. *Girtyella* widest at mid-length, with rounded anterior outline and rectimarginate commissure. Prominent ventral umbo with erect aperture. Inner hinge plates V-shaped both dorsally and anteriorly, supported by a low median septum extending anteriorly beyond the crural bases.

NAME. From Carrick Lough.

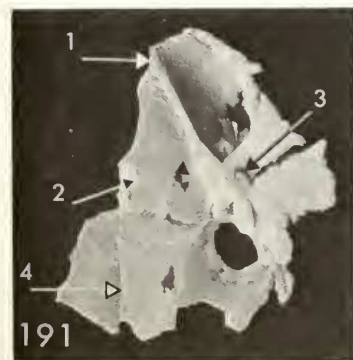
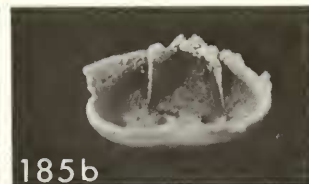
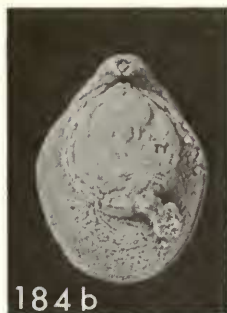
HOLOTYPE. BM(NH) specimen no. BB64000, Fig. 184a–c.

LOCALITY. The type locality is collection locality 14/4A at Carrick Lough, Co. Fermanagh, Ireland.

HORIZON. Probably early D₁, Asbian, Dinantian.

MATERIAL. About twelve specimens came from locality 14/4B (BB64025–BB64029, BB63033–63034), one hundred from the type locality 14/4A (BB64000–BB64009, BD186) and perhaps two specimens from the Milltown Bridge stream locality (BB63979), Co. Fermanagh. Thirty measured specimens range in length from 2.1 mm to 8.00 mm.

Figs 184–193 *Girtyella carrickensis* sp. nov., from Co. Fermanagh. Fig. 184a–c, **holotype** viewed ventrally, dorsally and laterally; the strong growth halt at about half the length is not a normal feature. From Carrick Lough. BB64000, $\times 3.75$. Fig. 185a, b, young ventral valve interior and internal umbonal regions showing the teeth and dental plates. From Carrick Lough. BB64004, $\times 7$. Fig. 186a, b, incomplete shell viewed laterally and dorsally. From Carrick Lough. BB64001, $\times 5$. Fig. 187a, b, incomplete young dorsal valve viewed internally and tipped posteriorly, showing the crural bases (one arrowed) on the ventral surfaces of the hinge plates. From Carrick Lough. BB64005, $\times 7$. Fig. 188, fragments of conjoined umbones viewed internally, showing the Y-shaped septalium, articulation and dental plates. From Carrick Lough. BB64003, $\times 5$. Fig. 189, incompletely silicified conjoined umbones showing growth lines on the dental plate (arrowed). From Carrick Lough. BB64002, $\times 7$. Fig. 190, dorsal valve interior, plus conjoined ventral valve umbo, with crura extending from the septalium. BB63033, $\times 6$. Fig. 191, incomplete conjoined umbones; dorsal valve uppermost with the median septum (arrow 1) of the septalium supporting the hinge plates, upon which the crural bases (arrow 2) can be distinguished. The tooth (arrow 3) and a dental plate (arrow 4) are preserved. BD186, S.E.M. $\times 15$. Fig. 192a, b, dorsal valve interior viewed dorsally and posterodorsally, showing the crura and a broken tooth in one socket (arrow). BB64026, $\times 7$. Fig. 193a, b, incomplete dorsal valve interior viewed dorsally and posterodorsally showing the full septalium. BB64025, $\times 6$.



DISCUSSION. The hinge plates, characteristic of *Girtyella*, in this species look more like those depicted in the *Treatise* (Williams *et al.* 1965) for *Fletcherithyris* than for *Girtyella*. It should be noted that the *Girtyella* illustration (1965: fig. 614.2b) is inaccurate if compared with the original sections illustrated by Weller (1911, 1914) for *G. indianensis* (Girty), the type species. From Weller's description it is clear that the hinge plates should be somewhat V-shaped, being depressed medially (Fig. 193). The dorsal median septum in the Fermanagh material is persistent from the umbo (Fig. 188) and the average punctal density, taken from six specimens, is 240 endopuncta per mm², much greater than to be expected in species of *Fletcherithyris*.

Girtyella carrickensis has an internally thickened pedicle aperture (Fig. 189) which, in larger specimens, may have developed into a pedicle collar. The dental plates are well developed (Figs 189, 194). No specimen has an adult loop preserved, but the origins and dispositions of the crura can be seen (Fig. 192). Young specimens, about 5 mm long, retain a simple centronelliform loop (Fig. 194). Measurements from 30 complete specimens from the Carrick Lough locality show that the species retained fairly consistent dimensions, width being about four-fifths the length and the height of the shell being half the length. Specimens commonly have well-marked growth halts on their valves (Fig. 184), several of which are about 2 mm from the anterior margin. It may be, therefore, that an important local event took place affecting the population and inducing a major growth halt in shell deposition. In comparison with studied living Terebratulacea (G. B. Curry, personal communication 1969), this marginal 2 mm of shell since the growth halt would represent approximately six months' growth.

The ventral umbo of no specimen shows signs of abrasion, so it is concluded that the species had a relatively long pedicle for attachment, or that the substrate for their attachment was insufficiently hard to abrade the shell. As no specimen could be shown to be exactly *in situ*, with respect to its enclosing limestone, it is impossible to tell which was the more likely, but shell debris in the sediment could have provided sites of attachment.

G. carrickensis externally resembles de Koninck's (1887: pl. 7, figs 7–10) species *Dielasma avellana*, but as he gave no information about internal morphology it is impossible to make a generic assignment of his specimens.

Species of *Girtyella* have seldom been recorded from western Europe. Muir-Wood (1951) suggested that *T. sacculus* J. de C. Sowerby might belong to the genus, but I believe the species normally lacks dental plates and has *Dielasma*-like cardinalia, so it should be assigned to *Balanoconcha* Campbell, known from Viséan strata of eastern Australia.

Family NOTOTHYRIDIDAE Likharev 1960

Genus ALWYNIA Stehli 1961

TYPE SPECIES. *Terebratula vesicularis* de Koninck, 1851: 666; pl. LVI, figs 10; a rare species from the Visé district of Belgium. Lectotype selected by Brunton (1982) (Fig. 195).

DIAGNOSIS (emended). Small Notothyrididae with anterior opposite or alternate folding. Puncta at about 200–250 per mm². No dental plates, small pedicle collar. Posteriorly perforate, unsupported cardinal plate.

DISCUSSION. Stehli (1961) assigned only the type species to the genus, recording it from the Viséan of Britain and Belgium. His generic diagnosis included an antiplicate anterior commissure, being the form of *A. vesicularis*. I treat this as a specific characteristic, broadening the generic diagnosis to include species having different commissural types, such as the rectimarginate, ligate form of *A. reidi* sp. nov. Judged from ten specimens of *A. vesicularis* (de Koninck) in the de Koninck collection of the British Museum (Natural History), it seems that the original figures of the species by de Koninck (1851: pl. 56, figs 10a–d) are uncharacteristic. These figures are of a species almost as wide as long, whereas nine of the ten specimens are consistently 2 to 3 mm longer than wide, at lengths of about 13 mm. The specimen from the Isle of Man illustrated by Stehli (1961: pl. 62, figs F1–5) is comparable to the de Koninck specimens, but differs in being slightly more strongly antiplicate and in having a slightly flatter dorsal valve.

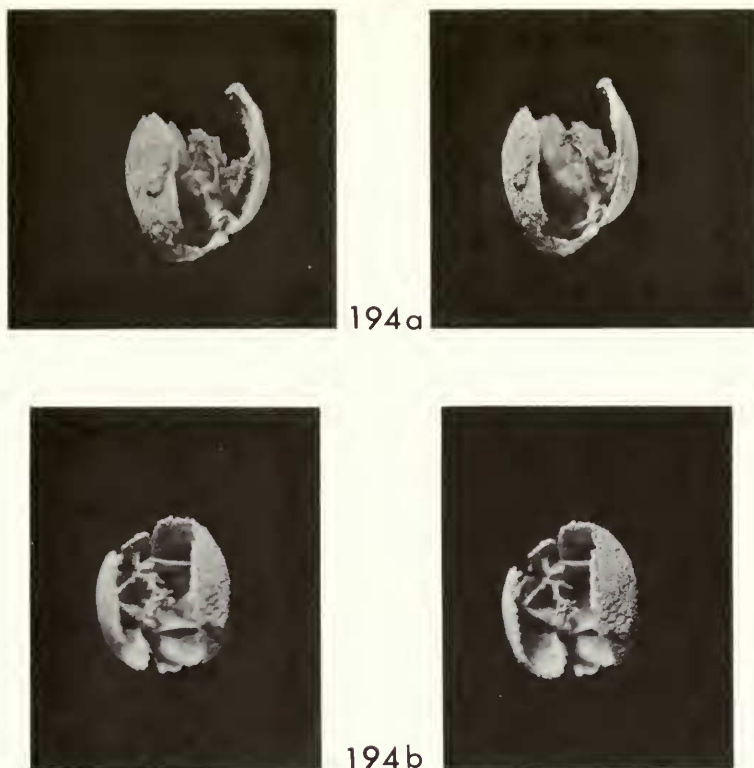


Fig. 194 *Girtyella carrickensis* sp. nov. from Carrick Lough, Co. Fermanagh; stereoscopic pairs. a, viewed posterolaterally, showing the brachial loop and articulation. b, viewed posteriorly, showing the loop in relation to the cardinalia. BB64006, $\times 6$.



Fig. 195 *Alwynia vesicularis* (de Koninck) from the Viséan of Visé, Belgium; selected as lectotype by Brunton (1982). Ventral, dorsal, lateral and anterior views. BD80, $\times 2.5$.

Alwynia reidi sp. nov.

Figs 196–199

1982 *Alwynia* sp.; Brunton: fig. 11.

DIAGNOSIS. Small (less than 10 mm long) *Alwynia* with rectimarginate anterior commissure and slight opposite folding, creating a ligate outline. Crural bases form ridges on dorsal surface of the hinge plate.

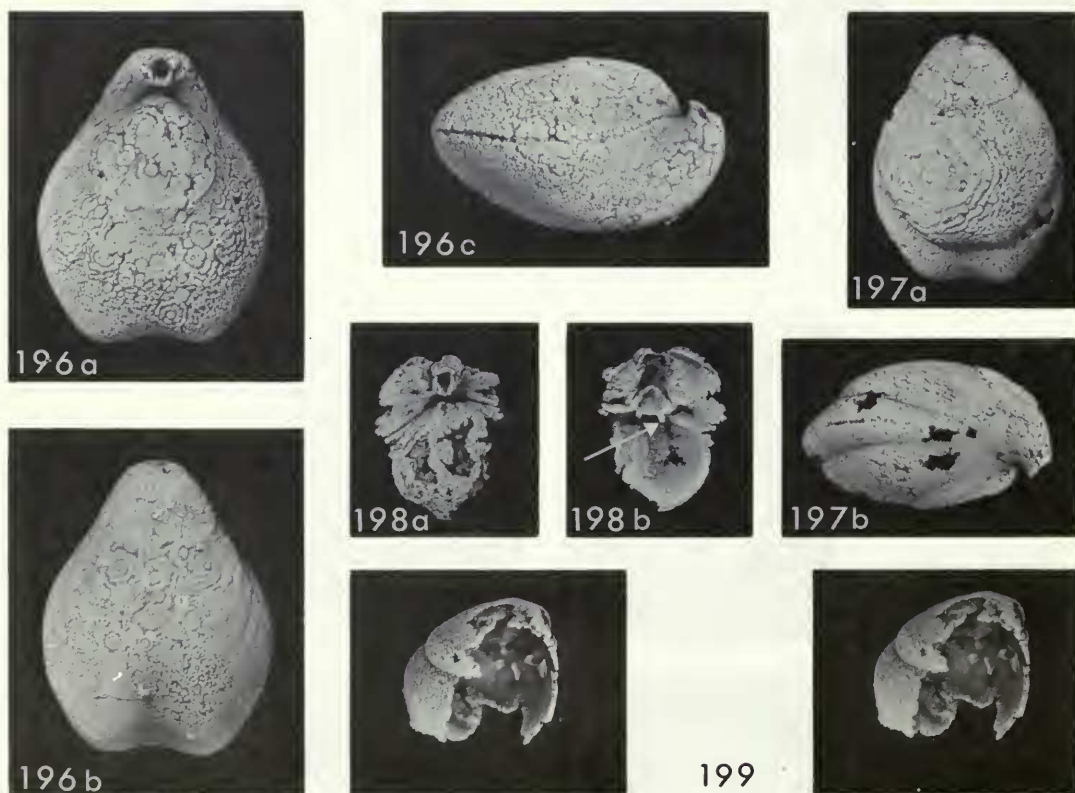
NAME. After R. E. H. Reid of Queens University, Belfast, who first acid-etched faunas from the type locality.

HOLOTYPE. BM(NH) specimen no. BB64046, Fig. 196a–c.

LOCALITY. Collecting locality 14/4B, near Bunnahone Lough, Co. Fermanagh.

HORIZON. The age of the limestones yielding the type specimen is thought to be early Asbian (D₁), Viséan.

MATERIAL. Ten specimens, mostly incomplete, came from the Carrick Lough locality (BB64010–BB64022); eight, including the holotype (Fig. 196a–c), from the Bunnahone locality (BB64046–BB64047, BD109–BD113); and about three incomplete specimens from the Milltown Bridge Stream locality (BB63980). All in Co. Fermanagh.



Figs 196–199 *Alwynia reidi* sp. nov., from Co. Fermanagh. Fig. 196a–c, holotype viewed dorsally, laterally and ventrally. BB64046, $\times 4.5$. Fig. 197a, b, shell from Carrick Lough viewed ventrally and laterally. BB64020, $\times 5$. Fig. 198a, b, conjoined umbones viewed externally and internally, showing crural bases (arrowed) extending from the hinge plate. From Carrick Lough. BB64022, $\times 6$. Fig. 199, stereoscopic pair of incomplete shell viewed posteriorly, showing the crura. From Carrick Lough. BB64021, $\times 4$.

DESCRIPTION. Small *Alwynia* with equibiconvex lateral profile, rectimarginate anterior commissure and a ligate outline. The ventral valve sulcus developed from a length of about 5 mm (Fig. 196b). Internally, the pedicle collar is most fully developed ventrally. In the cardinalia the inner socket ridges are strong and in plan view form a rounded V-shaped structure by posterior fusion near the indistinct cardinal process (Fig. 198b). The sockets are supported by lateral shell thickening and the unsupported median hinge plate has a small posterior perforation.

DISCUSSION. In the past virtually any dielasmatacean with a folded ventral valve, from the Dinantian, was called *Dielasma sacculus* (J. de C. Sowerby), and at first I thought this was the taxon for the Fermanagh species. Externally the shapes of the two species are similar, although Sowerby's species has a uniplicate anterior commissure and its widest part is nearer the front than in *A. reidi*. The clear difference, however, is internal; the inner hinge plates of *Terebratulula sacculus* form an open V to the valve floor, in a fashion characteristic of *Balanoconcha*, while in *A. reidi* the hinge plate is horizontal and unsupported between the inner socket ridges (Figs 198b, 199). The new species differs from *A. vesicularis*, the type species, in lacking the anteriorly-developed plications on the ventral valve which contribute to the antiplicate anterior commissure (Fig. 195a, b). Judged from Stehli's (1961) serial sections and drawing, the cardinalia are very similar, indeed the more so from his sections than from the drawing which, incorrectly, shows the crural bases forming ridges along the ventral surface of the hinge plate.

Two of de Koninck's 1887 'species' look externally similar to *A. reidi*, one called *Dielasma finale* (1887: 24), the other *D. gemmula* (1887: 29). The second is the more similar and, if the specimens exist and prove to belong to *Alwynia*, it might be conspecific with the Fermanagh species. *D. gemmula* came from late Viséan rocks of the Visé region, Belgium.

Superfamily **DIELASMATACEA** Schuchert 1913

Family **DIELASMATIDAE** Schuchert 1913

Genus **BALANOCONCHA** Campbell 1957

TYPE SPECIES. *B. elliptica* Campbell, 1957, from the Watts district of New South Wales, Australia. Originally it was dated as being of Tournaisian age, but more recent revisions of the stratigraphy of eastern Australia assign the rocks to zones 4 to 6, correlating with mid to upper Viséan of Europe.

DISCUSSION. The genus is included here, despite not occurring in the Fermanagh faunas, because it was thought initially that one of the species may have belonged within *Balanoconcha*, and investigations demonstrated for the first time that the genus exists in Britain.

Alwynia reidi sp. nov. (p. 114) externally somewhat resembles the species *Terebratulula sacculus* J. de C. Sowerby, so it was important to find the genus to which this species belonged. Muir-Wood (1951) selected a Sowerby specimen, BM(NH) no. B61653, as lectotype; writing that it had a single dental plate and a dorsal median septum, she suggested that it be assigned to *Girtyella*.

A re-examination of the lectotype of *T. sacculus* (see Brunton 1982: fig. 14) leads me to believe that it had only one 'plate' (perhaps a pathological structure or even a piece of shelly debris, such as part of the loop, lodged in the umbo) in the ventral valve. The serial sectioning of three specimens from Narrowdale, Staffordshire, within a few miles of the Derbyshire localities given for *T. sacculus*, shows that the normal condition of the species is to lack dental plates. Furthermore, the cardinalia are not Y-shaped in transverse section, as are those of *Girtyella*, but somewhat V-shaped, with the V opening anterodorsally as in *Balanoconcha*.

Terebratulula sacculus J. de C. Sowerby should, therefore, be assigned to *Balanoconcha*. There is a second species, from late Viséan rocks in Britain, which was called *sacculus* and figured by Sowerby (1824: pl. 446, fig. 1) on the same plate as the lectotype of *B. sacculus*, but this is smaller and much more strongly folded. It belongs to the genus *Harttella* Bell, 1929, and is described in my general review of British Dinantian terebratulides (Brunton 1982: 50).

Family **HETERALASMINIDAE** Likharev 1956Genus **BEECHERIA** Hall & Clarke 1894

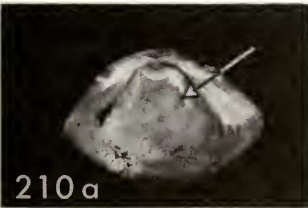
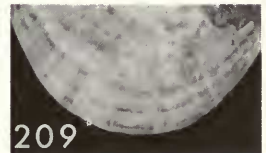
TYPE SPECIES. *B. davidsoni* Hall & Clarke, 1893.

DISCUSSION. The genus was first separated from *Dielasma* in the mistaken belief that it was devoid of dental plates. In his fine study of the Windsor Group faunas Bell (1929) discovered dental plates in the type species, *B. davidsoni*, and assigned it to *Dielasma*; at that time the significance of the different cardinalia had not been recognized. It was this difference that Stehli (1956) used in reviving *Beecheria*, but as pointed out by Campbell (1965), Stehli's sections, purporting to be of *Beecheria*, do not seem to be of the type species from the Windsor Group of Nova Scotia. Campbell (1965: 53) obtained specimens from there and produced serial sections which are probably a truer representation of the species, and genus. They match the Fermanagh material and show that the dorsal valve umbo does not have a short median septum (as on Stehli's sections), but that once the hinge plates lose contact with the inner socket ridges they continued to grow anteriorly as a diverging pair of inverted V-shaped ridges. Furthermore Campbell (1965) showed that the median segments of the hinge plates unite as a delicate



Fig. 200 *Beecheria hastata* (J. de C. Sowerby). Lectotype selected by Parkinson (1952), viewed dorsally, ventrally and laterally. Arrow 1 points to a dental plate and arrow 2 to the impression of the posterior ends of the hinge plates. From the early Viséan of Limerick, Ireland. B61657, $\times 1$.

Figs 201–210 *Beecheria treakensis* sp. nov. Figs 201–207 from Co. Fermanagh, Figs 208–210 from Treak Cliff, Derbyshire. Fig. 201, ventral valve exterior. BB64040, $\times 2$. Fig. 202a, b, part of dorsal valve viewed dorsally and anteriorly, showing the cardinalia and ventrally disposed crura. BB64044, $\times 8$. Fig. 203a, b, incomplete dorsal valve interior viewed laterally and posteriorly; the cardinal process is arrowed and the inverted V-shaped hinge plates are clearly seen, including the crural base (arrowed). BD181, S.E.M. $\times 10$. Fig. 204, incomplete dorsal valve interior with a fragment of ventral valve attached at one tooth. BB64042, $\times 2.5$. Fig. 205, cardinalia of adult dorsal valve showing the cardinal process and sessile median septalium. BB64043, $\times 5$. Fig. 206, part of dorsal valve interior showing one elongate socket, outer hinge plate and part of the median septalium (arrowed). BB64045, $\times 3$. Fig. 207, incomplete ventral valve exterior viewed anteroventrally, to display the small teeth (arrow) and the labiate pedicle opening. BB64041, $\times 4$. Fig. 208a, b, internal mould of specimen from Treak Cliff. a, dorsal view with the positions of dental plates showing (arrowed), $\times 1$. b, oblique view showing the impressions of the hinge plates (arrow 1) and median septum of the septalium (arrow 2), $\times 2$. BD3. Fig. 209, anterior end of dorsal valve from Treak Cliff, displaying radial 'colour' banding. BD4, $\times 2$. Fig. 210a–e, **holotype** seen posteriorly, anteriorly, dorsally, ventrally and laterally; most of the shell is missing allowing the dental plates (arrowed) to show, as well as traces of the cardinalia in Fig. 210c. From Treak Cliff. BD1, $\times 1.5$.



septalium very close to the valve floor. This structure is repeated in the Fermanagh species (Fig. 205). Campbell assigned several dielasmid species, described by Weller (1914) from the Mississippi Valley, to *Beecheria*, including *B. arkansana* (Weller) which is similar to the Fermanagh species, although not conspecific.

Species of *Beecheria* have not previously been recorded from western Europe, although some of the species assigned to *Dielasma* by de Koninck (1887) should belong here (e.g. *D. tumidum* de Koninck). However, in my brief review of British Dinantian terebratulide genera (Brunton 1982: 53) I discussed the status of *Beecheria* and illustrated the interior of the true *B. hastata* species (Fig. 200) from a set of serial sections reproduced in their correct orientations by a computer program (1982: fig. 20). Those illustrations showed an interior closely comparable to the interiors seen in the Fermanagh silicified material.

Beecheria treakensis sp. nov.

Figs 201–211

- ?1887 *Dielasma tumidum* de Koninck: 12; pl. 2, figs 27–29.
- ?p.1887 *Dielasma avellana* de Koninck: 22; pl. 7, figs 7–10.
- ?p.1887 *Dielasma radiatum* de Koninck: 24; pl. 7, figs 39, 40.
- ?p.1887 *Dielasma itaitubense* (Derby) de Koninck: 26; pl. 5, figs 1–10.
- v. 1952 *Dielasma hastata* (J. de C. Sowerby) Parkinson: text-fig. 1, nos. 1, 2.
- 1982 *Beecheria* sp.; Brunton: figs 15, 18, 19.

DIAGNOSIS. Medium length (seldom more than 30 mm) *Beecheria* with approximately ovate outline and flattened dorsal valve, seen in lateral profile. Anterior margin smoothly rounded, with rectimarginate commissure.

HOLOTYPE. BM(NH) specimen no. BD1, from Treak Cliff, near Castleton, Derbyshire, collected by D. Ward. Fig. 210a–e.

HORIZON. The 'Brachiopod Beds', Lower Carboniferous, Asbian age (D₁).

MATERIAL. Twenty-three paratypes in the Ward collection (BD2–BD18). The species is not common in the Fermanagh faunas but thirteen specimens were recovered from the Sillees River locality (BB64040–BB64045) and eight from Carrick Lough (BB63996–BB63999); all the silicified specimens are fragmentary.

DESCRIPTION. These elongate *Beecheria* specimens vary somewhat in outline but their dorsal valves, especially over the umbones, are characteristically flat (Fig. 210e). The anterior margin is normally gently rounded, but rarely is almost straight. Only very rarely is the commissure slightly uniplicate. The ventral umbo is prominent, with a labiate (Fig. 207), dorsally-directed aperture. Radial colour banding may be preserved (Fig. 209).

Dental plates are short, being confined to the umbo, and in posterior view diverge only slightly (Fig. 210a). Adults have a small knob-like cardinal process (Figs 203b, 205) at the posterior apex of paired diverging hinge plates forming inverted Vs on the valve floor (Fig. 203) and, medially, a very low septalium bearing concentrically-ridged muscle scars separated by a low myophragm (Fig. 205). The sockets are elongate, at the valve margin, and unsupported. The density of endopuncta is approximately 90 to 120 per mm².

DISCUSSION. Exfoliation of the shell on some Treak Cliff specimen displays the short dental plates and fine shelly ridges in the dorsal valve typical of the *Beecheria cardinalia* (Fig. 208a, b). These structures are well seen in the Irish silicified material (Figs 202–205), from which it is also clear that the outer plates are stronger than the inner and give rise directly to the crura. As the crura separate from their bases they form ventrally slightly divergent and deep shelly portions of the posterior loop (Fig. 202); however, the full loop is not preserved in this material.

B. treakensis resembles the type species, *B. davidsoni*, in several internal characteristics, including the general form of the crura and their bases. Bell (1929) described the rudimentary dorsal median septum and plate for muscle attachment between the crural bases, such as is seen well on some Fermanagh specimens (Figs 204, 205). *B. davidsoni*, according to the illustrations

provided by Bell (1929: pl. 23, figs 8–10, 15–18), which include the lectotype, is a fatter species, having a more normally convex dorsal valve, as seen in lateral profile. The two species are, however, closely related and this is not surprising since *B. davidsoni* comes from the Windsor Group of Nova Scotia, commonly correlated with mid to upper Viséan rocks of Europe. Bell's commonest occurrence of *B. davidsoni* is recorded as his B and C levels of the Windsor Group and he correlated the junction between these levels as at the start of the British D Zone, the Asbian. Thus the species appears to correlate with late Holkerian to early Asbian, close to the age of the Fermanagh fauna. Brunton & Mason (1979) commented on the relationships of Fermanagh sabkha-like Meenymore rocks to those of eastern Canada and the likelihood of the two areas having been closer in Carboniferous times than today. However, Jansa, Mamet & Roux (1978) concluded that the microfaunas of the two regions precluded a close geographical relationship and suggested the existence of a 'deep ocean or sea (that) separated Ireland from eastern Canada during the Viséan' (1978: 1428). Since several of the brachiopods described by

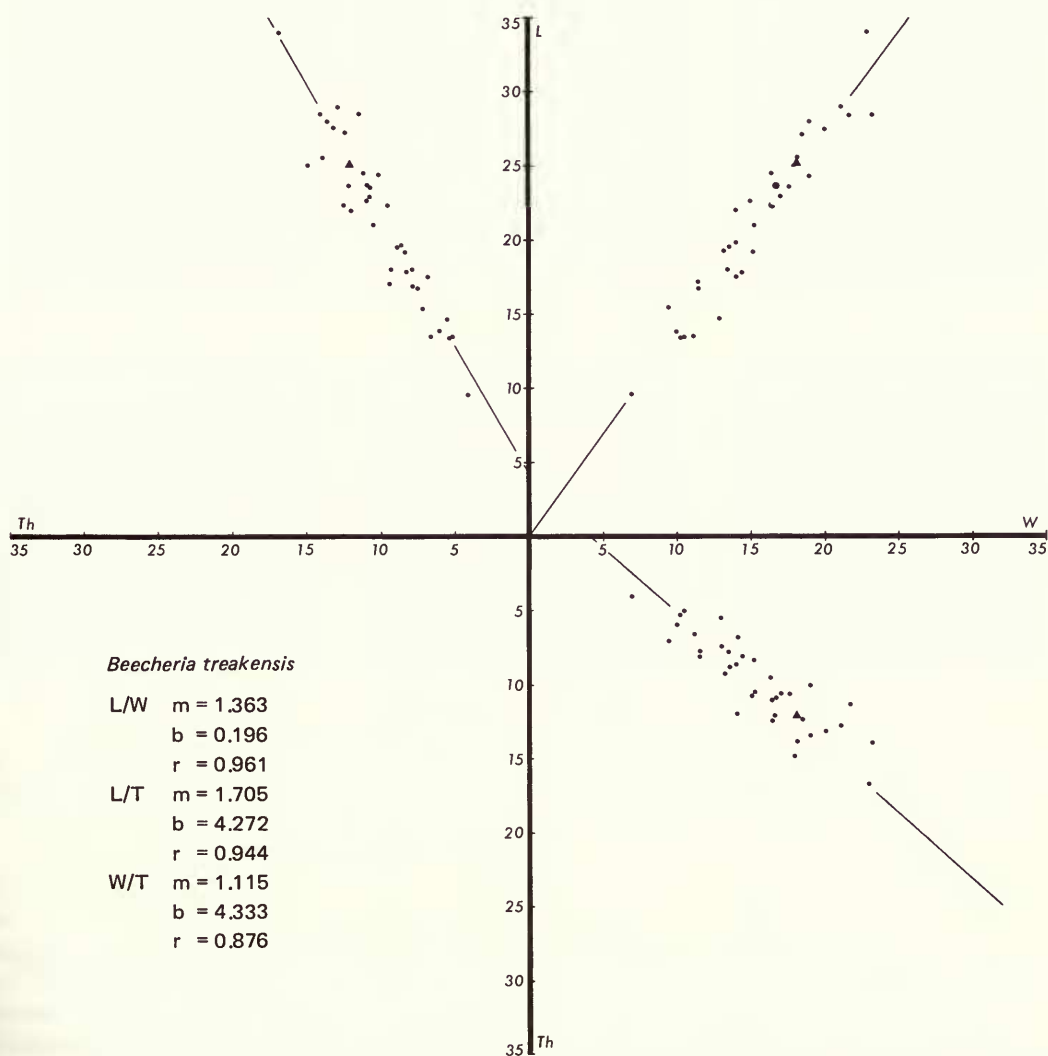


Fig. 211 *Beecheria treakensis* sp. nov. Length, width and thickness plots of 38 specimens from Treak Cliff, Derbyshire; holotype = $\blacktriangle$. m = slope of regression line; b = intersection point of m with axis; r = coefficient of correlation.

Bell (1929) from the Windsor Group resemble European Viséan species morphologically, it seems that we have something of a conflict. The late Viséan evaporitic deposits may have accumulated on opposite sides of a deep sea, which stopped benthonic microfaunal migration, but which developed only early in the Viséan, allowing some brachiopods to flourish on both shelves while retaining similar morphologies. Certainly by Namurian times the brachiopods were diverging, to become increasingly European or North American in character.

Beecheria species in the European Carboniferous are probably relatively common. The possible de Koninck (1887) synonyms include some specimens which undoubtedly are *Beecheria* species (e.g. *B. tumidum*), but the information on these Belgian specimens is insufficient to allow sure synonymy. In addition most of de Koninck's species names have not been reused and so should be considered as forgotten names (*nomina oblita*). For these reasons, and the lack of precision in their localities and horizons, I have not resurrected a de Koninck species name. *Beecheria hastata* (J. de C. Sowerby) is the common species in earlier Viséan rocks, the type specimen coming from probable Arundian rocks of the Limerick area of Ireland (Fig. 200a–c). The previous 'sack' use of *Dielasma hastata* has included specimens of *B. treakensis*, as, for instance, the two largest specimens of the series drawn in outline by Parkinson (1952) (but note that he exaggerated the uniplication in his second specimen, BM(NH) no. BB14869, attributed here to *B. treakensis*). Most of his other specimens are *Balanocoencha sacculus* (J. de C. Sowerby); none is *B. hastata*! It seems probable that serial sectioning or dissection to reveal the cardinalia of several European Carboniferous terebratulides will result in emendations of their generic assignments. Both *Dielasma* and *Beecheria* have dental plates, but it is generally easy to distinguish dorsal valves from which the shell has exfoliated posteriorly: *Dielasma* shows only the two traces of the inner hinge plates against the valve floor, whilst *Beecheria* displays the four traces of both the outer and inner hinge plates, with connections to the inner socket ridges only in the apex of the umbo. The diversity of *Beecheria* may prove greatest in the Carboniferous and of *Dielasma* in the Permian.

Appendix 1

The development of samples from the Sillees river locality since the publication of my paper on the productoids (1966a) has revealed seven examples of an additional species, briefly described below since interiors can be seen for the first time.

Family MARGINIFERIDAE Stehli 1954

Genus *EOMARGINIFERA* Muir-Wood 1930

Eomarginifera derbiensis (Muir-Wood)

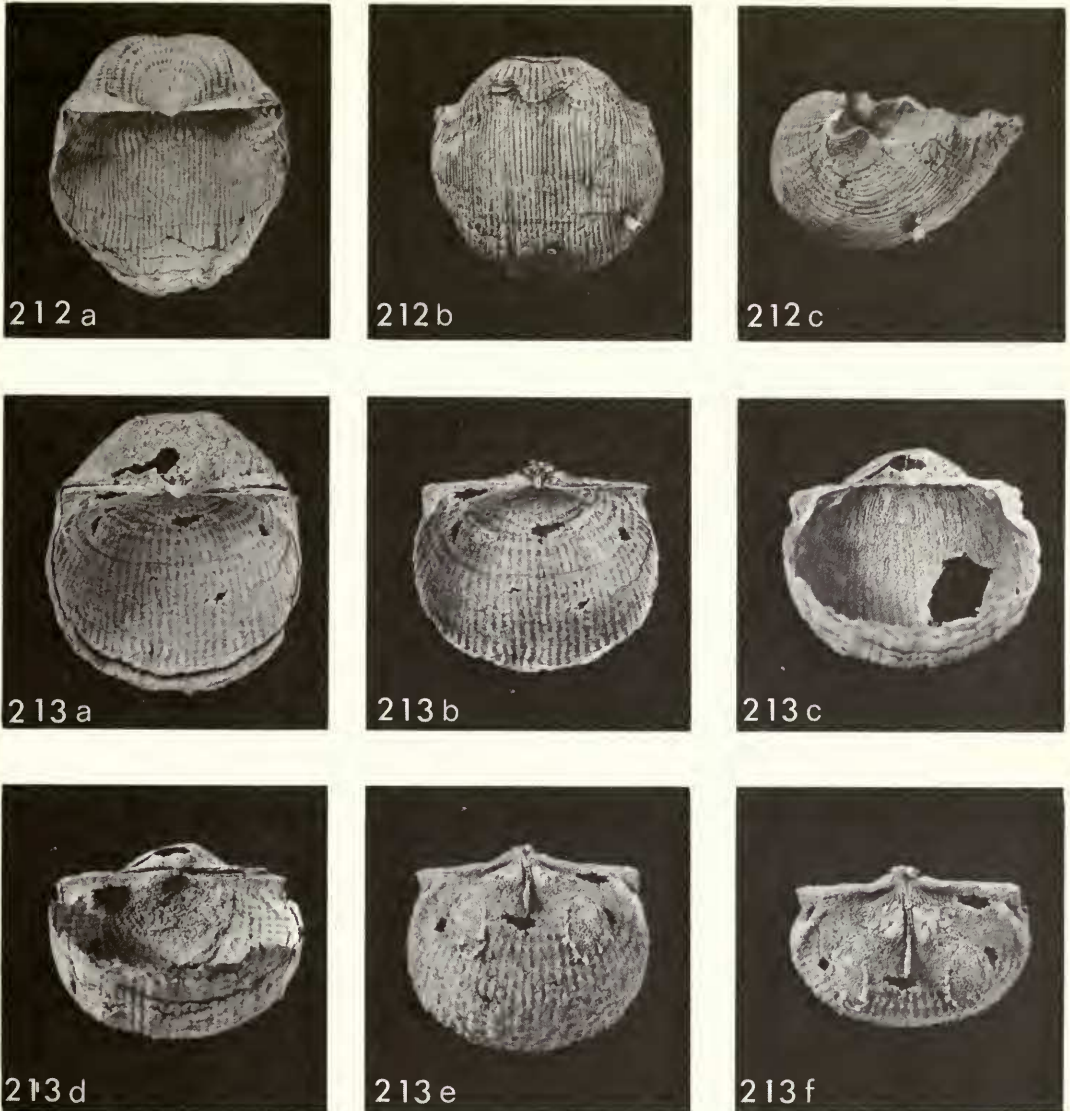
Figs 212–213

v* 1928 *Productus derbiensis* Muir-Wood: 170; pl. 11, figs 10, 11, 19a–c.

DIAGNOSIS. Medium to large eomarginiferids with rounded, non-geniculate, lateral profile and no median sulcus. Close, well-defined, ribbing (about 9 in 5 mm width at 10 mm from ventral umbo), with accentuated ribs on flanks by strongly differentiated small ears.

HOLOTYPE. BM(NH) specimen no. B43730, from Thorpe Cloud, Derbyshire (Muir-Wood 1928: pl. 11, fig. 10).

DISCUSSION. In 1928 Muir-Wood figured two specimens as *P. derbiensis*, the holotype and a second from Wetton, Staffordshire, BM(NH) no. B45516, which she called a 'Giganteid Form' (pl. 11, figs 19a–c). The maximum width of the holotype is 18.6 mm, while this large specimen is 25.5 mm wide. Because of its greater size this Wetton specimen has more major spines than the holotype, with an extra pair and a median spine on the ventral venter. The Fermanagh specimens display a similar range in size with one complete ventral valve at 16.9 mm maximum width, one at 21.2 mm (Fig. 212) and the largest at about 29.5 mm (one ear is missing). Again,



Figs 212–213 *Eomarginifera derbiensis* (Muir-Wood) from the Sillees river, Co. Fermanagh. Fig. 212a–c, posterodorsal, ventral and lateral views of a complete shell. BB64648, $\times 1.5$. Fig. 213a–f, complete shell. a, posterodorsal view of complete shell. b, posterodorsal view of dorsal valve alone, showing the cardinal process. c, interior view of ventral valve, showing the anterior ends of the diductor muscle scars. d, anterodorsal view of complete shell. e, internal view of dorsal valve. f, internal view of posterior region. BB64649, $\times 2$.

while details of the spine patterns anterior of the rugose areas differ, in other respects the specimens seem conspecific.

In her original description Muir-Wood was unable to describe the shell interior, but the Fermanagh material includes some complete disarticulated valves displaying their internal morphologies (Fig. 213c, e, f). This is typically marginiferid in its broad, sessile cardinal process, anteriorly high brevisseptum, raised dorsal adductor scars, clear brachial ridges and shelly ridges across the ears. However, no anterior marginal ridge appears to have developed (Fig. 213e).

Muir-Wood's original (1928) wide stratigraphical range for the species was later (Muir-Wood

& Cooper 1960) restricted to the Viséan, but I think the range should be further restricted to mid and upper Viséan, especially the Asbian and Brigantian stages.

Eomarginifera derbiensis differs from *E. lobata* (J. de C. Sowerby) or *E. setosa* (Phillips) in its finer ribbing and lack of median sulcation.

Appendix 2: List of brachiopod species

The full list of brachiopods recognized from the two localities (on the Sillees river and at Carrick Lough, Fig. 1, p. 29) is given below. An indication of the relative abundance of the various species is provided: a very rare (vr) species has fewer than five individuals; a rare (r) species between 6 and 20 individuals; a species is termed present (p) if represented by 21–50 individuals; common (c) if between 51 and 100 individuals, and abundant (a) if over 100 individuals. In addition ‘+’ indicates high numbers in the category, and ‘–’ indicates low in the category. The counts were based upon estimates of complete specimens, ignoring the numerous fragments of valves.

Described in 1968 (Brunton 1968):

<i>Crania quadrata</i> (M'Coy)	r
<i>Acanthocrania</i> cf. <i>laevis</i> (Keyes)*	r
<i>Philhedra trigonalis</i> (M'Coy)	r
<i>Schizophoria resupinata dorsosinuata</i> Demanet	p+
<i>Rhipidomella michelini</i> (Léveillé)	c+
<i>Leptagonia analoga</i> (Phillips)	r+
<i>Brochocarina wexfordensis</i> (Smyth)*	p
Orthotetidin [<i>Apsocalymma</i> MacKintosh 1974]	vr
<i>Serratocrista fistulosa</i> Brunton	p
<i>Schellwienella radialis</i> (Phillips)*	r
<i>Globosochonetes parseptus</i> Brunton*	a+
<i>Rugosochonetes silleesi</i> Brunton*	a
<i>Rugosochonetes delicatus</i> Brunton*	r+
<i>Rugosochonetes transversalis</i> Brunton*	r
<i>Plicochonetes buchianus</i> (de Koninck)	r

Described in 1966 (Brunton 1966a):

<i>Heteralosia</i> cf. <i>fortispinosa</i> (Hinchey & Ray)	c–
<i>Dasyalosia panicula</i> Brunton*	c+
<i>Dasyalosia lamnula</i> Brunton	c+
<i>Acanthoplecta mesoloba</i> (Phillips)	r
<i>Plicatifera plicatilis</i> (J. de C. Sowerby)	p
<i>Productina margaritacea</i> (Phillips)	c+
<i>Overtonia fimbriata</i> (J. de C. Sowerby)	c–
<i>Avonia</i> (<i>Quasiavonia</i>) <i>aculeata</i> (J. de C. Sowerby)	c+
<i>Krotovia spinulosa</i> (J. Sowerby)*	a+
<i>Krotovia lamellosa</i> Brunton*	a–
<i>Eomarginiferina trispina</i> Brunton*	a+
<i>Echinoconchus</i> cf. <i>punctatus</i> (J. Sowerby)	r–
<i>Pustula</i> cf. <i>pyxidiformis</i> (de Koninck)	vr
<i>Antiquatonia</i> sp.	r
<i>Ovatia</i> sp.	vr
Chonopectinid [description in preparation]	vr
<i>Eomarginifera derbiensis</i> (Muir-Wood) [see p. 120]	p

Herein:

<i>Propriopugnus pugnus</i> (Martin)	vr
<i>Pleuropugnoides pleurodon</i> (Phillips)	r
<i>Tretorhynchia trilatera</i> (de Koninck)	p+
<i>Coledium seminulum</i> (Phillips)	r
<i>Hustedia radialis</i> (Phillips)	a+
<i>Hustedia ulothrix</i> (de Koninck)	r

<i>Actinoconchus lamellosus</i> (Léveillé)	r
<i>Cleiothyridina fimbriata</i> (Phillips)*	c+
<i>Cleiothyridina deroissei</i> (Léveillé)	p+
<i>Crurithyris urei</i> (Fleming)	a+
<i>Nucleospira carlukensis</i> (Davidson)	p+
<i>Cyrtina hibernica</i> sp. nov.*	a+
<i>Tylothyris laminosa</i> (M'Coy)*	p
<i>Fusella rhomboidea</i> (Phillips)	r
<i>Skelidorygma integrigosta</i> (Phillips)	vr
<i>Spiriferellina insculpta</i> (Phillips)	c+
<i>Merospirifer linguifera</i> (Phillips)	vr
<i>Phricodothyris verecunda</i> George	p-
<i>Minythyra lophia</i> sp. nov.	r+
<i>Minythyra ernea</i> sp. nov.	p-
<i>Cryptonella minranensis</i> sp. nov.*	c
<i>Girtyella carrickensis</i> sp. nov.*	c
<i>Alwynia reidi</i> sp. nov.*	r
<i>Beecheria treakensis</i> sp. nov.	r

A small collection of silicified specimens was developed from a limestone, lower in the Glencar Limestone, which crops out in the stream draining east from the Black Slea forest area to Lower Lough Erne at Holme Bay. The locality is about 610 m south-west from Milltown Bridge and about 1465 m WNW of Church Hill, near Derrygonnelly, Co. Fermanagh. Seventeen of the above species (*) were recognized in this *Schellwienella*-rich argillaceous limestone. In the text this locality is termed Milltown Bridge Stream.

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